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DEVELOPMENTAL MORPHOLOGY OF THE GROWING POINT OF THE SHOOT AND THE INFLORESCENCE IN GRASSES [1]

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INTRODUCTION

Many thoroughgoing studies have been made of the development of the grass spikelet, flower, and caryopsis, and of the homologies of the floral parts, but the inception and early development of the inflorescence have received comparatively little detailed investigation. This lack, which exists for other plants as well as for grasses, has been recognized by various botanists (*52, p. 922; 78, pp. 112–113*).[3]

The object of the present investigation was to bring together and summarize as much as possible of the pertinent literature; to trace the morphological changes that take place in a growing point during its transition from the vegetative to the reproductive phase of its development; and to extend and clarify the knowledge of the initiation, organization, and early development of the inflorescence of a number of representative grasses.

This investigation originated about 1920 at the Timothy Breeding Station, North Ridgeville, Ohio, as an outgrowth of an earlier study of the life history of timothy. After 1922 the investigation was continued in the botanical laboratory and greenhouses of Oberlin College, Oberlin, Ohio. Since 1935 some of the observations and illustrations have been made at the Ohio Agricultural Experiment Station, Wooster, Ohio.

REVIEW OF LITERATURE

The previous studies on the early development of the inflorescence of grasses may be conveniently grouped under the following headings: Structural Morphology, Physiological Morphology, and The Plastochrone.

STRUCTURAL MORPHOLOGY

The most extensive of the studies on structural morphology are contained in 6 papers by Trécul (*68, 69, 70, 71, 72, 73*), published in 1880. The first and last papers report comparative studies of the

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[3] Italic numbers in parentheses refer to Literature Cited, p. 515.

developmental succession of branches and spikelets in the inflorescences of 20 or more genera of grasses. The other papers deal with the order of appearance of the primary vessels in the rachis and spikes in 6 genera. Trécul (*68*) described the leaf primordia of the nascent inflorescences of grasses as "bourrelets" or "collars," and the branch primordia, i. e., the secondary protuberances, as "mamelons." He stated that in many species of grasses the primary axis of the inflorescence has its merithalles marked by distichous rudimentary leaves that ordinarily encircle the axis in the form of collars which are higher on the dorsal side, more rarely half-encircling in the upper part of the very young axis. These collars diminish in size as they occur higher and higher on the rachis, and the rachis is often free of them in its upper region. Trécul also state that in *Phleum pratense* L. and in a large number of other grasses the branches develop in succession from above downward on the lower part provided with collars, while they develop acropetally toward the tip.

Goebel (*28*), in 1884, studied the development of the spikelet in 13 genera, and described briefly, and illustrated, early stages in the development of the inflorescence of *Alopecurus ruthenicus* Weinm., *Setaria italica* (L.) Beauv., and *Cenchrus echinatus* L. In his discussion of the latter species, he described the manner in which the protuberances branch and produce shoots of successively higher orders. The following is a translation of his description:

> Each axis of the second order produces two rows of branches. Thus there arises, first of all, a lateral branch to the right and to the left; each of these lateral branches branches again in a plane which crosses the plane of branching of the mother-axis.

Extending the observations of Wigand (*83, p. 90*), published in 1854, Goebel in 1884 (*28*) and 1931 (*30*) has divided the inflorescences of the Gramineae into two types, "dorsiventral" and "radial," the former having their lateral primordia distichous in the same plane as the primordia of the preceding foliage leaves and vegetative buds, the latter having them polystichous. He found the dorsiventral type to be by far the more general. Wigand gave *Zea mays* L. as the only member of the radial type known to him. To this Goebel added *Setaria*, *Cenchrus*, and *Chloris radiata* (L.) Swartz. As examples of "falsely radial" inflorescences, Goebel named *Alopecurus* and *Phleum*, since in these the arrangement of the branch primordia is actually distichous and dorsiventral although the mature inflorescence takes on the appearance of radiality. In the present paper, evidence will be presented indicating that the so-called "radial" type of Wigand and Goebel is also merely "falsely radial."

Trécul described three kinds of developmental succession of lateral primordia in the incipient inflorescence. Goebel, however, saw these as merely three modifications of the developmental relations of acropetally originating organs. These three relations were:

(1) Acropetal primordia and acropetal development, occurring only in the "radial" type of inflorescence: e. g., in *Setaria* and *Zea*.

(2) Acropetal primordia and basipetal development, occurring in *Milium effusum* L., *Poa annua* L., *Glyceria fluitans* (L.) R. Br., *Nardus*, etc.

(3) Acropetal primordia and "a speeding up" of development in the middle region of the inflorescence axis, so that development is basipetal below this region, but acropetal above it, as in *Secale cereale*, *Alopecurus ruthenicus*, and *Phleum pratense*.

Observations on these types of developmental succession are presented in this paper.

Weber (*80, 81*) has recently published two important papers on the origin and early development of the inflorescence of a large number of grasses. He uses the terms acrotony, basitony, and mesotony to designate Trécul's three kinds of development.

Since the work of Trécul and Goebel incidental observations on the origin and early development of the inflorescence of certain of the Gramineae, chiefly cereals, have been made by a number of workers, as adjuncts to other studies. Among these are observations on barley by Lermer and Holzner (*43*) in 1888; on wheat, by Carruthers (*15*) in 1892, Hays and Boss (*33*) in 1899, Jensen (*37*) in 1918, and Kiesselbach and Sprague (*39*) in 1926; on *Hordeum distichum* L. and *Alopecurus geniculatus* L. by Schuster (*66*) in 1910; on wheat, rye, and barley by Schneider (*61*) in 1912; on *Poa pratensis* L., *Phleum pratense*, and *Setaria italica* by Nishimura (*46*) in 1922; on *Oryza sativa* L. by Yamasaki (*87*) in 1928; and on *Monerma repens* Beauv., *Stenotaphrum subulatum* Trin., and *Cornucopiae cucullatum* L. by Helm (*34*) in 1934.

In his description of the nascent inflorescence of wheat, Schneider (*61*), recognizing the relationship of the leaf primordia and the secondary protuberances which they subtend, said: "On the axis of the spike, leaves continue to be initiated. In their axils the primordia of the spikelet axes appear as rounded humps."

Studies have recently been made by Bonnett on barley (*5, 8*) in 1935 and 1938, on wheat (*6*) in 1936, on oat (*7*) in 1937, and on corn (*9*) in 1940, all illustrated with photomicrographs. In his first paper on barley, Bonnett (*5*) correlated the stage of morphological development of the growing point or rudimentary inflorescence with the number of leaves on the shoot; in his paper on wheat he correlated the stage of development with the date on which it was observed.

Noguchi (*47*), in 1929, made an exhaustive statistical study of the developmental changes in the primary shoot in 10 genera of grains, and illustrated and discussed briefly the early stages in the development of the inflorescence and flower. He regarded the apical growing region of the shoot, from the germination of the seed to the expansion of the inflorescence, as the "inflorescence-primordium," treating its development under (*a*) its growth and (*b*) its morphological change.

In the present study, stage *a* is referred to as the "vegetative phase" and stage *b* as the "reproductive phase" or as "the initiation or inception of the inflorescence."

PHYSIOLOGICAL MORPHOLOGY

The effects of various environmental conditions, as, for example, soil nutrients (*22, pp. 14–16*), length of day (*24*), and temperature (*23, fig. 1*), on the vegetative and reproductive development of plants have long occupied the attention of physiologists.

More recently the developmental "aftereffects," induced by temperature, by the photoperiod, and by certain other conditions during germination and early seedling stages, have been extensively studied. Kidd and West (*38*), in 1919, reported on a number of these "induction" conditions and their aftereffects.

In grasses "photoperiodic induction" at germination and its aftereffect during the transition from vegetative to reproductive develop-

ment have been studied especially by Rasumov (*53*) in 1930 and by Lubimenko and Ščeglova (*44*) in 1931.

Similarly, "thermo-induction," or the aftereffect of germination temperature, in relation to the flowering of cereals, has been studied by a number of investigators (*1*, *27*, *45*, *48*). Most of these studies however, have failed to give attention to the fundamental conditions of meristem activity and primordium differentiation.

Purvis (*52*) in 1934 found in winter rye that both short days and low temperature at germination caused an increase in the rate of growth of the apical meristem, and that short days also favored the development of leaves, so that together they brought about an extension of the meristematic cylinder and increase in leaf ridges.

Noguchi (*47*), on the other hand, hinted at a genetic factor when he suggested that the elongated meristematic cylinder is characteristic of perennial forms, while the growing point which continues short and dome- or cone-shaped and in which only a few rudimentary phytomers accumulate, characterizes summer grains. He called the former "the winter grain type," the latter "the summer grain type."

In most of the studies the environmental condition has been regarded as having a specific effect that can be modified only slightly. Too little attention has been given to the anatomical condition of the plant preceding reproduction (*55*, *85*), to the plant's inherent developmental sequences and rhythms (*61*), and to the extent to which genetic and hereditary characters determine the plant's responses to a given environmental factor (*54*, *pp. 675–676*).

In this connection Noguchi (*47*) found that in six species of summer grain the average number of days after seeding, before the morphological changes which initiate the inflorescence, ranged from 45 to 85. But in five winter grains he found that the approximate number of days after seeding before morphological changes occurred ranged from 145 to 175.

THE PLASTOCHRONE

Since the only reference to the plastochrone that has been noted in the American literature is a brief observation by Foster (*26*), in 1932, and since the concept seems to offer a valuable approach to the study of certain problems of growth, it has seemed wise to give a brief résumé of some of the more important European papers dealing with the subject.

The concept was enunciated and the term first employed by Askenasy (*4*) in 1880.

As a result of observations on the internodes of plants, Sachs had found that the more constant the environmental conditions the more uniform was the course of growth. With this as an assumption, Sachs (*57*), in 1873, selected a transverse zone 1 mm. long, lying close to the tip of a root, and measured its growth during successive equal intervals of time through its entire growth period. He found that the increment of growth of this tranverse zone during the equal time intervals differed in different parts of the growth period.

Askenasy reversed this procedure and studied the time intervals required to inaugurate equal, very short, transverse zones or segments of the shoot. He assumed that if growth is approximately uniform under relatively constant environmental conditions the growing point must initiate the extremely short members of the segmented

shoot at constant intervals of time. To this unit time interval he gave the name "plastochrone." He found that the absolute duration of a plastochrone differs in different plants, in different shoots of the same plant, and under different environmental conditions, but that under constant environmental conditions it is "a period of definite and uniform duration."

Almost simultaneously, Westermaier (*82*), in 1881, attacked the same general problem, confining himself to a study of algae, hepatics, ferns, and fern allies, all of which have a single apical cell. A translation of his statement (*82, p. 454*) follows:

> As time units I chose the time that elapses from the appearance of one segment wall in the apical cell to the formation of the next succeeding segment wall. I call this time a step. The absolute duration of the time which a step requires is immaterial.

Klein (*40*), in 1884, made an intensive study of the segmentation of the apical cell in 11 species of ferns. He found that the "pace" of apical-cell segmentation is very inconstant.

These approaches to the study of plant growth were almost completely ignored until 1916, when Schüepp (*63*) employed Askenasy's method, extended its application, and confirmed his conclusions.

Schmidt (*60*) in 1924, Schüepp (*64, 65, pp. 792, 793*) in 1926–27 and 1929, Foster (*26, pp. 78, 79, 94*) in 1932, and Priestley and Scott (*51*) in 1933 determined the plastochrone in various dicotyledonous plants.

Almost no studies have been made of the plastochrone in grasses. But Schüepp (*63*), in 1916, recorded the plastochrone of scale or catyphyll initiation in that form of *Bambusa verticillata* which he studied as 2.1 days. The temperature and other conditions of growth were not stated. The plastochrone, at least in some species of grass, may be less for those rudimentary phytomers of the inflorescence that are initiated after reproductive processes have begun than for those on the same axis that are initiated while the shoot is in a vegetative condition. Zimmermann (*88*), in 1928, has referred to the plastochrone in *Hypericum uralum*, and Kliem (*41, pp. 285, 286*), in 1937, to the plastochrone in *Avena sativa*.

General observations on the succession of leaf emergence in grasses have been made by different workers. For example (*22, p. 36*), on a number of timothy shoots observed from September 13 to December 9, a new leaf appeared on an average of once in 14.0 days. On another group of shoots observed from April 18 to May 29, when temperature and other conditions were more favorable for growth, the average interval between the appearance of new leaves was reduced to 9.8 days. The difference in the interval at which leaves emerged would suggest the probability of a difference in the plastochrone of phytomer inception and organization under the two conditions.

As the term is used in the present study, the plastochrone is the number of days required for the initiation and organization of a phytomer of a grass shoot up to the time a discernible leaf primordium has developed on it, not to the time of leaf emergence or expansion.

MATERIAL AND METHODS

The appearance of a young grass shoot such as timothy (*Phleum pratense*), when its growing point is at the stage corresponding with the description given below, is illustrated diagrammatically in figure 1,

which shows a plant whose growing point is located within the leaves near the base of the shoot and near the surface of the soil.

If the leaves of a young shoot are removed by means of a dissecting needle, the growing point may be found in the form of a minute,

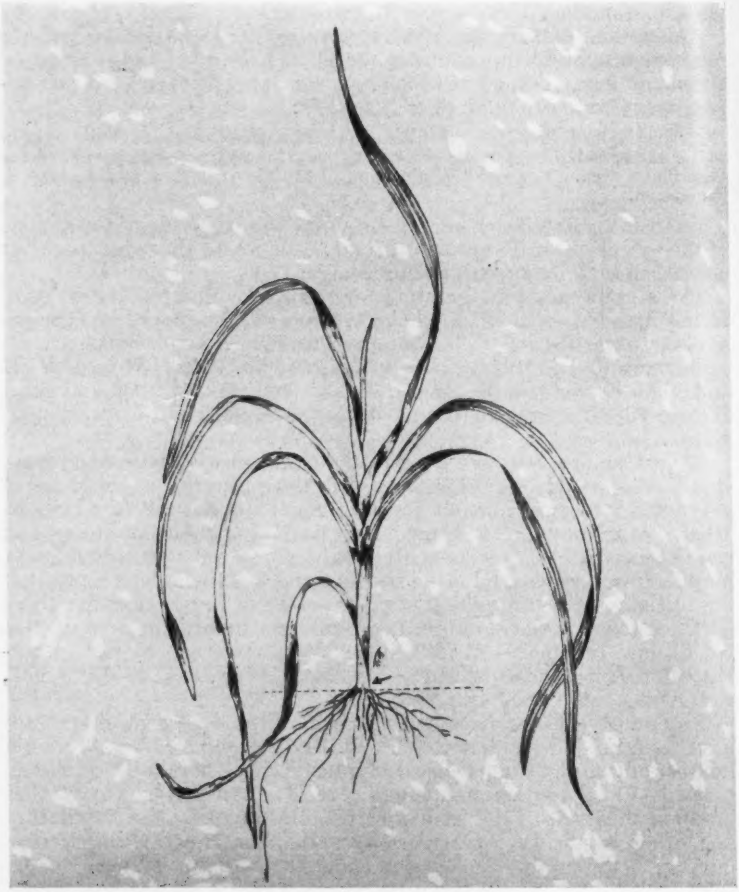

FIGURE 1.—Vegetative shoot of timothy. Dotted line at ground level; arrow directed to the growing point.

slender, often somewhat tapering, meristematic cylinder enclosed by the lower parts of the leaves that have developed.

Most of the illustrations are habit drawings from living material. The method of making them was to dissect away carefully the leaves at the base of the growing points of a number of shoots, to select one or more specimens suitable for illustrative use, and then to examine them under one of the lower powers of a compound microscope. In most instances the drawings were made with the aid of the camera

lucida. If the meristematic cylinder was in a comparatively early stage of development, all parts were drawn under the camera lucida. In older, less translucent and more complex stages, only the outlines were drawn with the aid of the camera lucida; the details were added without its aid. Some of the later drawings were made by the "double-vision" method, and others were entirely freehand.

Since considerable time was required for the study and illustration of a specimen, its tissues were likely to dry out gradually. To prevent this drying, microculture slides with the depression filled with water were used in some cases. The axis of the dissected specimen was severed just below the base of the cylinder by a very oblique cut. The specimen was then placed on the slide in a horizontal position with its base in the water cup. If a small amount of water was kept in the depression, the specimen received enough moisture to keep it in a normal condition, but the cylinder itself was above the water level; thus its appearance was not distorted. In other cases the specimen was supported horizontally on constantly moistened filter paper, the tip projecting beyond this above a film of water on the slide.

During the course of this investigation, a study was made of eight species, in as many genera, belonging to seven tribes (*36*).

GENERAL MORPHOLOGY AND TERMINOLOGY

In order to clarify the terminology employed in this paper, it will be necessary to present some of the conceptions of the morphological units of the vascular plants.

In accordance with the practice of Arber (*3*) and others, the root system and the "stem-leaf" or "shoot" system of Sachs (*58*, *59*) are regarded as the primary units of the plant.

The adult shoot system may be simple or compound. The "simple shoot" stage in the development of a seedling has been called the "primary shoot." But as Sachs (*59*, *p. 172*) observed, "it often happens that lateral shoots of any order take root and become detached from the primary shoot; they then assume all its peculiarities, and may equally be considered as primary shoots." The compound shoot system consists of the primary shoot plus one or more orders of lateral shoots.

Sachs (*59*, *p. 595*) extended his conception of the shoot to the inflorescence, where the leaves are generally reduced or otherwise modified as "hypsophyllary leaves or bracts" or "sometimes are entirely absent from the inflorescence or from certain parts of it." Goebel (*29*, *p. 433*), in 1905, supported this view. On the other hand, Dutailly (*19*), in 1871, insisted that in the Gramineae "the branches of the inflorescence are in no wise comparable to normal shoots." He based his conclusion chiefly on the behiavior of the vascular system in the branching of the inflorescence and of the foliage-bearing axes.

In this paper the terminology of Sachs is adopted, and the term "shoot" is used when referring to parts of the inflorescence as well as to the foliage-bearing parts of the plant.

Numerous attempts have been made to subject the "stem-leaf shoot" to analysis, with the object of establishing smaller and more basic units of morphological and physiological organization or of determining the direction of evolution of the complex shoot systems

now existing. For a presentation and review of some of the theories embodying these attempts, the following writers should be consulted: Velenovský (*74, pp. 550–551*), 1907; Cook (*17, pp. 172–176*), 1907; Bower (*10, pp. 134–138*), 1908; Arber (*3*), 1930; and Bower (*11, pp. 544–546, 617–634*), 1935.

For more than a hundred years the segments that compose the shoots of vascular plants have been variously designated as merithalles, phyton units, etc. A considerable number of somewhat different phytonic theories have developed, according to which the shoot is built up of a succession of shoot segments or phyton units, the phyton unit being the true individual. In 1879 Gray (*31, p. 7*) employed the term "phytomer" to designate one of these phyton units or "structures which, produced in a series, make a plant of the higher grade." More recently Weatherwax (*78, p. 40*), 1923, has amplified this definition thus:

"An internode together with the leaf at its upper end, and the bud at its lower end, constitutes a phytomer, the unit of structure of the shoot." The bud may be "small and poorly developed, or sometimes represented by only a meristematic region." He later (*79, p. 212*), 1930, added: "A single leaf arising from the upper end of each internode subtends a bud, or the primordium of one, which is borne in the embryonic region of the lower end of the internode next above it." The leaf and the bud of the same phytomer are therefore on opposite sides of the axis.

For the purposes of this paper the phytomer is accepted as the segmental unit of the plant. In their earliest stages the segmental units of a grass shoot are referred to as rudimentary phytomers.

From the standpoint of taxonomy, Hitchcock (*35, p. 117*) considered the spikelets to be the units of the inflorescences. However, in developmental morphology the phytomers of the inflorescence may be regarded as the units of organization just as the phytomers of which a vegetative shoot is composed may be regarded as the units of its organization.

VEGETATIVE GROWTH

THE GROWING POINT

The terminal growing point of the shoot, or the "vegetative point" of Wolff (*86*), is composed of an apical meristem. The youngest and least differentiated of its cells at the extreme tip of the shoot form the promeristem, from which are directly derived the primary meristems that give rise to the fundamental tissues of the shoot.

According to Douliot (*18, p. 93*), 1891, the promeristem and primary meristems of the growing point of grasses originate in two initial apical cells, the outer initial giving rise to a meristematic dermatogen while from the inner subjacent initial a primary meristem is derived that ultimately differentiates into plerome (central cylinder) and periblem (cortex). On the other hand, Porterfield (*49*), 1930, recognized in the growing point of black bamboo (*Phyllostachys nigra* Munro) four vertically seriated apical initials, the dermatogen and periblem being derived from the two most distal initials, the outer and inner tissues of the plerome from the two lowest.

Through the differential division and growth of the cells of the young plerome, periblem, and dermatogen, a succession of folds, or

ridges, result, as described by Schüepp (*62*) in 1914, Priestley (*50*) in 1928, and Priestley and Scott (*51*) in 1933. These ridges, arising in acropetal succession, constitute the first external indication of a segmental differentiation of the axis into regions composed of node and internode, that is, into the phytomers which constitute the segmented shoot. In grasses the ridges arise on alternate sides of the growing point, forming distichous rows. The apical growing point and elongating meristematic cylinder of the shoot are for convenience regarded as a "vegetative point" until the inception of the first protuberances of the nascent inflorescence. Schmidt (*60*), 1924, Buder (*12*), 1928, and Zimmermann (*88*), 1928, have replaced Hanstein's ambiguous concepts of plerome, periblem, and dermatogen with the concepts tunica and corpus; and Kliem (*41*), 1937, has made rigorous application of these concepts in his detailed study of the vegetative cone of *Avena sativa* and in his critical analysis of Rösler's (*56*) use of these concepts.

FIGURE 2.—Photomicrograph of a growing point of timothy at an advanced stage of the vegetative phase, showing distichous leaf ridges.

When a vegetative growing point is examined with the aid of a good pocket lens, from a direction coinciding with the median plane of the leaves, it appears somewhat translucent with transverse lines or ridges extending across it, giving the cylinder a segmented appearance, the lower ridges being somewhat more conspicuous than those above. When the cylinder is rotated 90° on its axis, it is found that the upper ridges do not completely encircle the cylinder and that they occur in two vertical rows placed 180° apart, the successive ridges alternating with each other. This alternate arrangement of ridges corresponds with the alternate and distichous arrangement of the leaves of the shoot. A photomicrograph of a meristematic cylinder of timothy in its late vegetative phase, viewed at right angles to the plane of the leaves, is shown in figure 2.

The vegetative growing point of grasses ordinarily measures from 0.5 to 1.0 mm. in length. In the species studied the growing points did not usually attain a length of 1.0 mm. until after they had passed the vegetative phase.

As in timothy, so in Kentucky bluegrass (*Poa pratensis*) and many other grasses, there is no internodal elongation of the stem until about

the time the growing point enters the reproductive phase. The result is that during its vegetative phase the growing point remains close to the surface of the ground. On the other hand, in certain grasses, such as Canada bluegrass (*Poa compressa* L.), even the earliest internodes of the shoot become slightly elongated (*25, p. 142*), so that the growing point is soon elevated somewhat above the position indicated in figure 1.

THE LEAF FUNDAMENT AND EARLY LEAF DEVELOPMENT

Each ridge, the origin of which is outlined above, makes rapid lateral growth until it completely encircles the axis as a somewhat oblique leaf primordium or leaf fundament. Meanwhile, the tissues of the lower or dorsal side of the ridge grow slowly, yet somewhat faster than do those of the upper or ventral side, until the ridge has a narrow free edge.

If conditions are favorable for foliage development the free edge of the ridge finally elongates in the middle region as a leaf-blade fundament. For the purposes of this paper, the leaf fundament is arbitrarily assumed to have become a young leaf when it exceeds 1 mm. in length and has enveloped at least half the axis.

DEVELOPMENT OF INTERNODES AND BUDS

The tissues of the very young phytomers, organizing just below the apical meristem, remain for a time in a highly meristematic condition with only slight structural differentiation. When further structural differentiation sets in, it does not occur uniformly and simultaneously throughout the phytomer. Instead, the cells of the more distal portion of the axis of each phytomer gradually mature and become changed into permanent tissues, while most of the cells of the basal region, in proximity to a node, retain their meristematic character for a long time and may continue to add new cells to the axis of the phytomer. The axis is thus composed of intercalary meristems separated from each other by maturing or mature tissues.

While the shoot is in the young vegetative condition a bud may organize from the intercalary meristem at the base of a phytomer, on the side opposite that on which the leaf of the phytomer originates. The bud is, therefore, in the axil of the leaf that crowns the phytomer next below.

LEAF DEVELOPMENT IN RELATION TO INITIATION OF NEW PHYTOMERS

In some species, as teosinte (*Euchlaena mexicana* Schrad.) and sugarcane (*Saccharum officinarum* L.), the development of the leaf primordia into foliage leaves may for a time, under certain conditions, almost keep pace with the formation of new phytomers by the apical meristem, and the vegetative point may thus retain its hemispherical or rounded conical shape.

In many species new phytomers are laid down by the apical meristem somewhat faster than leaf development progresses. This results in a gradual and sometimes rather large accumulation, below the undifferentiated vegetative tip, of successive phytomers with rudimentary leaf fundaments and thus in a progressive elongation of the growing point into a slender meristematic cone or cylinder above the origin of the most distal foliage leaf. The number of rudimentary

phytomers that eventually accumulate in the growing point varies widely in different species. For example, in this study there were found in perennial ryegrass (fig. 5, *B*) accumulations of as many as 17 rudimentary phytomers with more or less well-developed leaf fundaments. In quackgrass (fig. 3, *B*) and in timothy (fig. 9, *B*) the numbers may also become quite large. On the other hand, in orchard grass (fig. 14, *B*) only five or six rudimentary phytomers with leaf ridges were observed, and the growing points assume the form of a rather slender cone.

THE INFLORESCENCE

An inflorescence in grasses always terminates a vegetative shoot. The rachis is the central axis of the inflorescence (*14, p. 413*). A branch lateral to this primary shoot is called a secondary shoot of the inflorescence, or a shoot of the second order; one lateral to that is a tertiary shoot, or a shoot of the third order, etc.

The development of the parts of the inflorescence follows fundamentally, though with certain modifications, the same course as the growth of the vegetative parts of the shoot. Branchings occur, which may vary in number, in manner of growth, in the extent of elongation of their internodes, and in the type of spikelet and floret produced, the result being mature inflorescences of a great variety of form. Yet, notwithstanding this diversity in the form of the mature inflorescences, their early development is fundamentally the same.

TIME OF INITIATION OF INFLORESCENCES

The time when the growing point, or meristematic cylinder, undergoes the morphological change that definitely marks the initiation of the inflorescence varies with the species and variety, with the order of the shoot and its age, with nutritive and seasonal conditions, with the length of the daily period of illumination, with latitude, and with other factors.

In the latitude of northern Ohio, the growing point of most perennial grasses, as for example, timothy, ordinarily remains in a vegetative condition during late summer and fall and until April or very early in May of the following year. About this time there begins to be visible in the growing point certain morphological changes, indicative of changes in the physiological activities of the cells, that will result in structures predominantly reproductive in place of those predominantly vegetative.

In annual grasses, whose seeds germinate in the early spring, the inflorescences originate and develop somewhat later than do those of most perennial grasses.

At the time of "shooting," that is, when the inflorescence emerges from the enclosing leaf sheath, several weeks after the initiation of the inflorescence, the organization and most of the development of the inflorescence have been completed.

TRANSITION FROM VEGETATIVE TO REPRODUCTIVE PHASE OF THE GROWING POINT

In all species that have been studied, the transition from the vegetative to the reproductive phase is usually marked by a sudden and vigorous elongation of the growing point and by an increase in its diameter.

At about this time, in all parts of the growing point, further development of the leaf fundaments is stopped. However, in the proximal region they may remain as distinct ridges, even in the mature inflorescence. Throughout the middle region, where the ridges are younger and not so well formed, they may gradually become obliterated as the growing point expands in length and diameter, the obliteration beginning on the side of the axis opposite the one on which the midrib of each leaf would have developed (figs. 3, *C*; 9, *C*).

In the growing point of some species, such as perennial ryegrass (fig. 5, *B*) and timothy (fig. 9, *B*), both of which are perennials, there is during the vegetative phase a gradual accumulation of a relatively large number of rudimentary phytomers with leaf ridges, accompanied by a corresponding change from a conical to a cylindrical form. In the growing point of the inflorescences of some other grasses, as in the staminate inflorescence of teosinte (fig. 18, *A*, *B*, and *C*), during the vegetative phase there is an accumulation of only a limited number of phytomers with leaf ridges and the growing point has a conical form up to about the time that transition to the reproductive phase occurs. There is then a rapid elongation of the externally undifferentiated meristem above the leaf ridges, and the growing point rather suddenly assumes a cylindrical form. In a third group of species, the growing points never become entirely cylindrical though they may approach that form. They remain more nearly conical. Orchard grass (fig. 14, *B* and *C*) is included in this group.

BEGINNINGS OF THE INFLORESCENCE

The morphological change in the growing point that marks the definite inception of the inflorescence is the formation of lateral swellings or protuberances at the base of some of the rudimentary phytomers. The first protuberances to appear are formed in the axils of the most recently organized and least developed leaf fundaments, and at corresponding positions by the next more distal phytomers that lack leaf fundaments.

Each of these protuberances represents a lateral growing point and may be regarded as the homologue of the primordium of a vegetative bud (*6, p. 449; 52*). Since it is the primordium of a secondary shoot, or a shoot of the second order of an inflorescence, it may be called a secondary protuberance. In order to emphasize the pronounced morphological differences between the encircling ridge growth of the leaf-base fundaments and the very localized swellings of the primordia of lateral shoots, the latter will be referred to hereafter simply as protuberances. These secondary protuberances are the fundaments of the foundational skeletal structure of the inflorescence.

In timothy and in many other grasses, a large proportion of the phytomers of the nascent inflorescence have more or less well-developed leaf ridges at the time when secondary protuberances begin to form. In such species the number of rudimentary phytomers with leaf fundaments varies with the time the shoot has had for vegetative growth before the initiation of the inflorescence in the spring.

Distal to the region of inception of the earliest protuberances, the apical meristem continues for a time to organize new phytomers acropetally. As each phytomer reaches a certain stage of organization it gives rise to a secondary protuberance at its proximal end

without forming a leaf fundament at its distal end; the successive protuberances, therefore, alternate with each other distichously, as is illustrated by the uppermost phytomers in figure 7, *C*. The number of secondary protuberances arising from the hitherto externally undifferentiated apical region of the growing point differs in different species, varieties, and races. This may result in a mature inflorescence most of whose secondary shoots (primary branches) originated in this acropetal succession of protuberances without subtending leaf fundaments. In the inflorescences of other grasses most of the secondary shoots of the inflorescence develop from phytomers with leaf fundaments that accumulated before the inception of the inflorescence.

Simultaneously with this acropetal development, there occurs downward a successive activation of localized meristems, previously dormant, which results in the appearance of protuberances in the axils of successively lower leaf fundaments (figs. 3, *E*; 7, *E*). The strength of this activation lessens basipetally with the more pronounced vegetative organization of the phytomers, the protuberances that arise being successively smaller. In other words, each of the more proximal phytomers in these rudimentary inflorescences is still so physiologically and structurally plastic that the character of its growth activity gradually becomes altered to such a degree that it finally initiates the primordium of a secondary shoot of the inflorescence instead of continuing the growth of the leaf it had already originated. However, the sexualization of the very lowest phytomers of an inflorescence is so greatly delayed and is so incomplete that they are able to form only small, often imperfect or sterile spikelets.

The nascent inflorescence presents the anomaly of having protuberances originating in acropetal succession in the distal region of the meristematic cylinder and at the same time in basipetal succession in the proximal region.

The earliest protuberances at the middle region of the nascent inflorescence begin to develop further before the acropetal and basipetal formation of new protuberances is completed (figs. 3, *E*; 7, *E*).

In most grasses the apical meristem ends its activity by forming a more or less perfect terminal spikelet; but in some cases its activity may cease without the formation of a spikelet (*6, p. 449; 32, p. 177*).

Growth of Secondary Protuberances in Relation to Development of Leaf Primordia

During the vegetative phase of the development of a growing point, that part of each leaf primordium from which the midrib of the blade would develop is usually somewhat higher than the opposite part from which the overlapping free edges of the sheath would develop.

Figure 5, *C* and *D*, shows views of a very young rudimentary inflorescence of perennial ryegrass. Most of the phytomers have formed leaf fundaments; a protuberance has formed in the axil of each of the leaf fundaments except the two lowest. The leaf fundament and the protuberance to which the same number has been given have developed from the same phytomer. The uppermost protuberance has no subtending leaf fundament.

The corresponding stage in orchard grass (fig. 14, *C*) shows more clearly that the strong development of a protuberance at the base of a phytomer is accompanied by the elongation of that side of the phytomer, so that the slope of the leaf fundament at distal end of the

phytomer is reversed. This is well illustrated in phytomers 2, 3, and 4. If the leaf primordium at the distal end of the phytomer is weakly developed, the vigorous growth of the protuberance may obliterate the overlapping parts of the primordium whereas the midrib region still persists, as is seen in phytomer 5 (*l. pr.* 5 and *sec.* 5). Distal to this, the phytomers have formed only protuberances or the leaf fundaments have been completely obliterated.

Change in Physiological Balance From Vegetative to Reproductive Activity

From the structural relations outlined above, it seems clear that the phytomers in the lower part of any typical nascent inflorescence were being organized while the growing point was in a strongly vegetative state; that during the organization of the middle part, progressive internal changes toward the reproductive state were taking place so that further development of the leaf fundaments of these phytomers was stopped soon after their initiation; and that in the distal part of the rudimentary inflorescence the growing point was in a strongly reproductive state, so that each phytomer organized a protuberance but no leaf fundament (fig. 7, *C, D, E, F*). These figures seem to indicate in the lower part of the primary shoot two physiological and structural gradients running in opposite directions. The first gradient, that of vegetative activity manifesting itself in the origin and development of foliage leaves, passes with lessening strength from the base distally. The second gradient, that of reproductive activity, manifests itself first in the production of protuberances in the middle of the inflorescence, and passes downward for some distance with decreasing strength.

Plants With Once-Branched Inflorescences

Once-branched inflorescences are morphologically the simplest and develop when the secondary protuberances—primordia of the secondary shoots of the inflorescence—do not give rise to lateral protuberances of a higher order, but each instead merely initiates at its distal end a single spikelet. In such an inflorescence all the spikelets are of the second order, terminating shoots of the same order, except the one which may terminate the primary shoot and which is therefore a primary spikelet, or spikelet of the first order.

Typical examples of once-branched inflorescences are those of quackgrass and ryegrass. The pistillate inflorescence of teosinte (see fig. 20) is also once-branched.

The primary spikelets of both once-branched and multiple-branched inflorescences have their glumes and lemmas in the plane of the foliage leaves and of the secondary protuberances of the primary shoot (figs. 3, *F;* 5, *E* and *F;* 7, *F;* 9, *G*). The distichous order of the secondary spikelets is continued distally in the arrangement of the glumes and lemmas of the terminal spikelet, its lowest glume being on the opposite side of the rachis from the uppermost secondary spikelet. In its early organization, the terminal primary spikelet is somewhat precocious. The primordia of its glumes and lemmas are usually laid down somewhat in advance of those on the one, two, or three secondary spikelets immediately below it, and often some time before the secondary protuberances at the base of the inflorescence have begun to be organized.

QUACKGRASS

In most once-branched inflorescences, and also in most or all of the multiple-branched inflorescences, the glumes and the lemmas of the

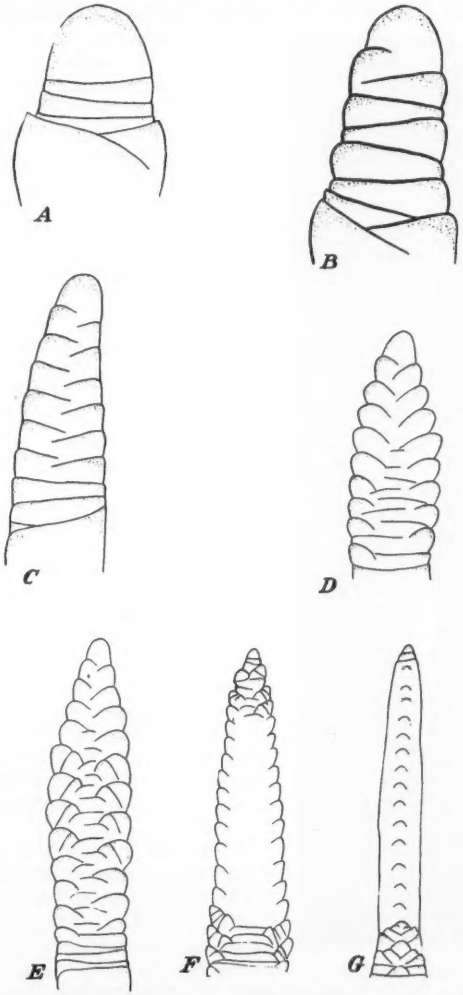

FIGURE 3.—Quackgrass: *A–F*, Seen at right angles to the plane of the leaves; *G*, in the plane of the leaves. *A*, Growing point of a young vegetative shoot, 0.7 mm. long; *B*, more advanced vegetative growing point, 0.9 mm. long; *C*, transition stage, protuberances about to form, 1.0 mm. long; *D*, secondary protuberances forming; *E*, glume primordia on the older protuberances; *F* and *G*, two views, at right angles to each other, of an inflorescence in a late stage of organization, partly in outline, glumes and lemmas forming.

secondary spikelets develop in a plane at right angles to the plane of the leaves of the shoot. This arrangement of the parts of the second-

ary spikelets is typified, for the once-branched inflorescences, by quackgrass (*Agropyron repens* (L.) Beauv.). Vegetative growing points and nascent inflorescences of this species are illustrated in figure 3, *A–G*.

The earliest indication of spikelet formation occurs when ridges develop on the protuberances, like those on the older protuberances in the middle part of figure 3, *E*. Later, additional ridges form (fig. 3, *F* and *G*). The first ridge is the fundament of the lower glume, the second of the upper glume. Other ridges become the lemmas, which develop in acropetal succession above the glumes. Afterwards protuberances develop in the axils of some or all of the lemmas, as illustrated by the early protuberances in the axils of the first and second lemmas in the terminal spikelet in figure 3, *F*. From these protuberances in the axils of the lemmas, the florets form.

A fully developed inflorescence of quackgrass is shown in figure 4.

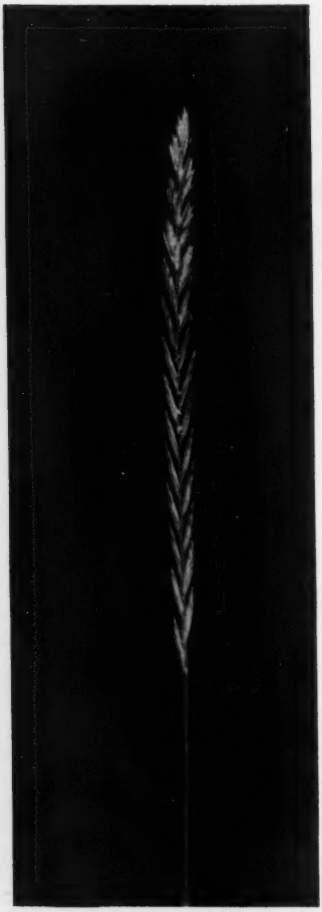

FIGURE 4.—Inflorescence of quackgrass soon after it has emerged from within the enclosing leaf sheaths

PERENNIAL RYEGRASS

In the once-branched inflorescences of *Lolium*, unlike those of quackgrass and most other grasses, the glumes and lemmas of the secondary spikelets originate and develop in the same plane as the leaves of the primary shoot and as the glumes and lemmas of the terminal spikelet. Vegetative growing points and nascent inflorescences of perennial ryegrass (*Lolium perenne* L.) are illustrated in figure 5, *A–F*.

A mature inflorescence of perennial ryegrass is shown in figure 6.

On the lateral spikelets of the rudimentary inflorescences of perennial ryegrass, the primordium of the first glume, the position of which would be next to the rachis, has been suppressed. However, according to Goebel (*29, p. 397*).

In *Lolium temulentum*, especially in the lower flowers of the inflorescence, it is frequently developed, seldom as an entire leaf, but usually replaced by two small leaflets, which are separated from one another by a broad intervening space.

The rudimentary inflorescence shown in figure 5, *E*, had 25 phytomers producing lateral protuberances or spikelets, as compared with

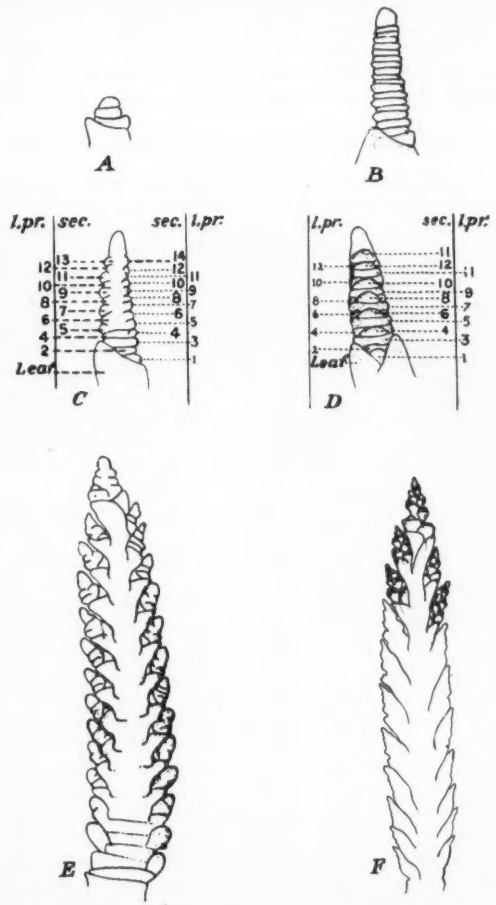

FIGURE 5.—Perennial ryegrass: *A*, *B*, *C*, *E*, and *F*, Viewed at right angles to the plane of the leaves; *D*, in the plane of the leaves. *A*, Growing point, early vegetative stage; *B*, growing point, late vegetative stage, with 17 rudimentary phytomers below a relatively long, still undifferentiated apical meristem; *C* and *D*, two views at right angles to each other of a very young rudimentary inflorescence just after the transition from the vegetative phase. *l. pr.*, leaf primordia; *sec.*, secondary protuberances. Most of the phytomers have formed leaf fundaments; protuberances that are fundaments of spikelets have formed in the axils of all of the leaf fundaments except the two lowest. The leaf fundament and the protuberance having the same number have developed from the same phytomer; *E*, a middle stage of rudimentary inflorescence; basic skeleton complete with inception of terminal spikelet; lateral spikelets organizing acropetally and basipetally from the middle region; *F*, late stage in organization of the inflorescence; florets forming in the axils of the older lemmas.

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only 19 in the more advanced specimen illustrated in figure 5, *F*. On any particular date during the period of initiation and formation of inflorescences, different stages of development may be found. At the same stage of development, there may be a considerable range in the number of phytomers of which the inflorescences are composed. Similar variations have been observed in the other grasses studied.

PLANTS WITH MULTIPLE-BRANCHED INFLORESCENCES

In grasses that are more than once-branched, as canary grass, timothy, orchard grass, and others, each secondary protuberance, soon after it is formed, begins to elongate somewhat and to organize tertiary protuberances along its length distichously and acropetally. These are in a plane at right angles to the plane of the secondary protuberances (fig. 7, *D* and *E*). From the "lateral" faces of the tertiary protuberances, as they in turn elongate, quaternary protuberances may develop acropetally, and so on for the higher orders (figs. 9, *F* and *G;* 14, *F*).

FIGURE 6.—Perennial ryegrass: Mature inflorescence, showing the glumes and lemmas in the same plane as the leaves of the shoot.

Thus a much-brached inflorescence may result, having each successive order of shoots at right angles to those of the next lower order. The number of orders of protuberances, and therefore of branches of the inflorescence, differs with the species and in a general way is characteristic of the species. As a rule, however, in the species studied the number of orders did not exceed four or five.

The extent of internodal elongation in the inflorescence differs greatly in different species. In some it is so nearly negligible that heads and spikes of a compact character result, as in canary grass and in timothy, giving "falsely radial" inflorescences (*28*). In many others the internodal regions of some of the phytomers, both of the primary shoot and of its branches, elongate to such an extent as to form axes of considerable length. This may result in loose and often relatively large inflorescences, as, for example, the inflorescences of tall oatgrass and orchard grass, and the staminate inflorescence of teosinte.

Organization of the latest and youngest protuberances of a given order does not necessarily precede the initiation of protuberances of the next higher order. Instead, before the youngest secondary protuberances have been initiated, tertiary protuberances begin to form on the older secondaries and even quaternary protuberances may have

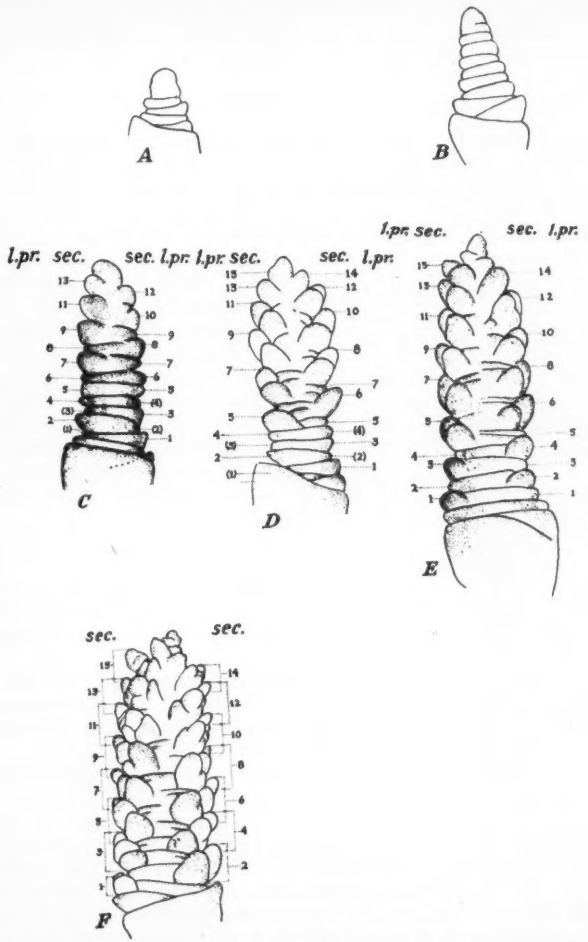

FIGURE 7.—Canary grass: All figures at right angles to the plane of the leaves; leaf primordia (*l. pr.*) and secondary protuberances (*sec.*) that are a part of the same phytomer have the same number assigned to them. *A*, Growing point of a young vegetative shoot; *B*, growing point at an advanced vegetative stage; *C*, a very early stage in the initiation of an inflorescence; the three proximal phytomers of the inflorescence proper, like the uppermost culm phytomers, are well advanced in vegetative organization; *D*, tertiary protuberances forming on the older secondaries; *E*, the terminal spikelet organizing its two glumes; the beginnings of quaternaries at phytomers 11 and 12; *F*, primordia of lemmas on terminal spikelet and of glumes on older lateral spikelets. For convenience in the correlation of *C*, *D*, *E*, and *F*, the structures that are a part of or arise from corresponding phytomers are given the same numbers. If at a certain stage a particular phytomer has not yet initiated the secondary protuberance which the corresponding phytomer of another older shoot shows, as in *E*, *secs.* 1, 2, 3, and 4, then the potential but not yet developed secondary of the younger stage is given the corresponding number enclosed in parentheses, as in *C* and *D*, *secs.* (1), (2), (3), and (4).

begun to form on the older tertiary protuberances. Thus, protuberances and ultimately spikelets of all orders may be forming simultaneously in different parts of the inflorescence.

Canary Grass

Different stages in the development of growing points of canary grass (*Phalaris canariensis* L.) are illustrated in figure 7, *A–F*.

In figure 7, *F*, the lateral groups arising from phytomers 10 and 11 appear to be the most advanced. Acropetally from these the groups from phytomers 12, 13, 14, and 15 are less and less advanced, although most of these seem to be nearer the stage of spikelet organization than are any of those below phytomer 10. The rudimentary terminal primary spikelet is more advanced than any of the lateral ones developing from secondary protuberances. Below phytomer 10, the development of the lateral groups is basipetally less and less advanced, decreasing as the size of the subtending leaf base increases.

A fully developed inflorescence is shown in figure 8.

Figure 8.—Inflorescence of canary grass

Timothy

Vegetative growing points and nascent inflorescences of timothy (*Phleum pratense*) are illustrated in figure 9, *A–G*.

Photomicrographs of four representative stages in the development of the timothy shoot and inflorescence are shown in figure 10, *A–D*.

A fully developed inflorescence of timothy is illustrated in figure 11, *A*.

In a small percentage of inflorescences of timothy, the leaf fundament crowning the uppermost internode of the culm, such as the one next above the basal leaf fundament in figure 9, *C–D*, may have a prolonged development and produce a short leaf sheath, with a more or less well-formed blade, subtending the group of spikelets of the most proximal phytomer of the mature inflorescence. Figure 11, *B*, illustrates this.

Tall Oatgrass

The development of the vegetative growing point and of the young inflorescence of tall oatgrass (*Arrhenatherum elatius* (L.) Mert. and Koch) is shown in figure 12, *A–F*.

The vegetative growing points of the primary shoots of tall oatgrass gradually become cylindrical in form, not greatly unlike those of quackgrass and perennial ryegrass. The final number of phytomers of which it is composed does not become so great as in the two other species mentioned, both of which are once-branched. Instead, in tall

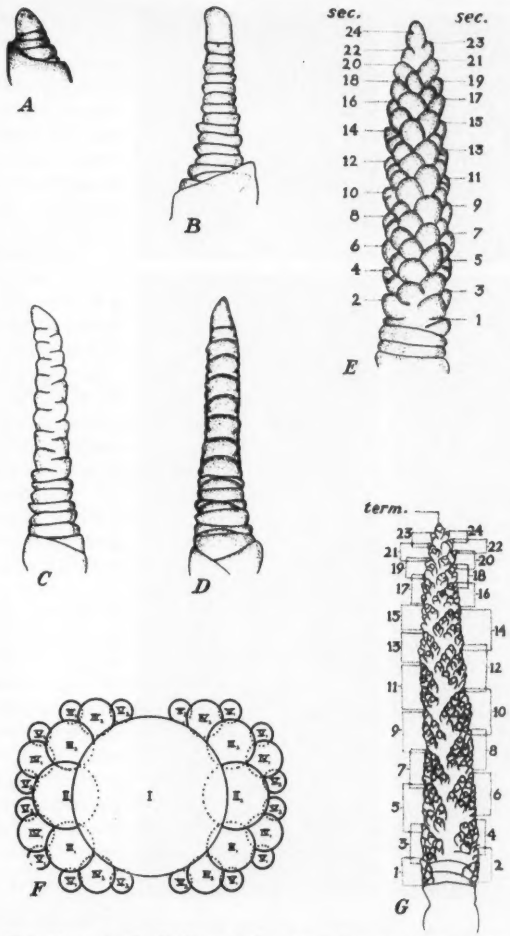

FIGURE 9.—Timothy: *A*, *B*, *C*, *E*, and *G*. viewed at right angles to the plane of the leaves; *D*, in the plane of the leaves. *A*, A young, cone-shaped vegetative growing point; *B*, a cylindrical growing point at a late stage of the vegetative phase; *C* and *D*, two views of a nascent inflorescence just after the transition from the vegetative phase; the right of *C* is the face of *D*; the relatively large, well-established leaf fundament at the base crowns the second internode of the culm below the inflorescence; the next higher leaf fundament crowns the uppermost internode of the culm; *E*, a middle stage in the organization of the inflorescence; formation of inflorescence phytomers and of secondary protuberances nearly complete; tertiaries forming but not quaternaries; *sec.*, secondary protuberances; *F*, diagrammatic vertical projection of cross sections of two successive phytomers of a young inflorescence of timothy, showing the arrangement of protuberances of different orders. The rachis is represented by I; two secondary axes by II_1 and II_2; and two axes of each higher order which have originated from each secondary one by III_1, III_2, IV_1, IV_2, V_1, and V_2. As these subsequent orders of protuberances develop, they become crowded from the positions which they otherwise might occupy; *G*, late stage in the organization of the inflorescence; inception of terminal spikelet (*term.*) and of lateral spikelets of different orders; all structures within a single bracket originated from one phytomer.

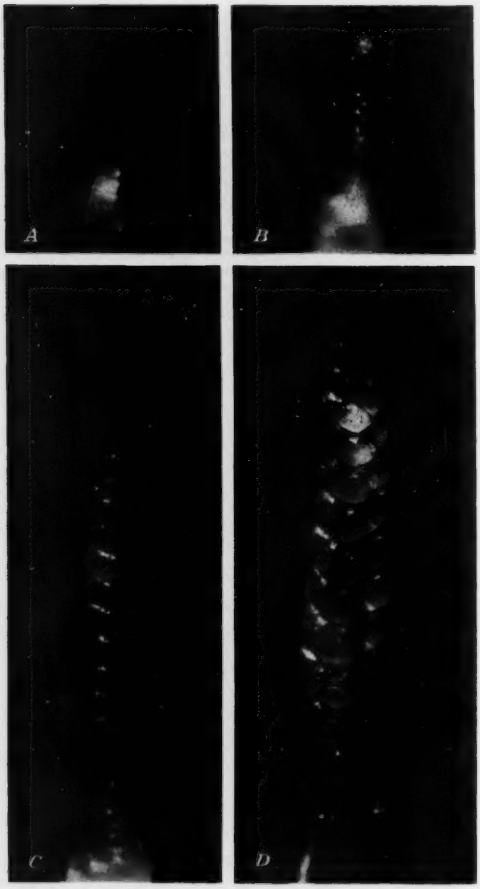

FIGURE 10.—Timothy: Photomicrographs of vegetative growing points and young inflorescences, all viewed at right angles to the plane of the leaves and of the secondary protuberances. *A*, Young vegetative growing point at a slightly more advanced stage than the one illustrated in figure 9, *A; B*, growing point at about the time of transition from vegetative to reproductive phase—about the stage illustrated in figure 9, *C; C*, a nascent inflorescence with secondary protuberances throughout the middle region; *D*, a young inflorescence in which the two rows of prominent protuberances in the foreground are tertiaries, developed on the flanks of the two rows of secondaries seen less clearly in the background on the extreme left and right.

oatgrass provision for multiplication of spikelets is made through the development of branches of higher orders rather than through a continued increase in the number of secondary spikelets.

Tall oatgrass illustrates a phenomenon common among grasses with loose inflorescences, in which the proximal phytomer or phytomers of the secondary branches do not always elongate; some of the tertiary and even quaternary branches may remain grouped at the bases of the secondaries, forming clusters or pseudowhorls of branches at the nodes of the rachis. The more distal internodes of the branches, however, lengthen considerably, giving rise to an inflorescence of the paniculate type (fig. 13).

ORCHARD GRASS

In the inflorescences of many species of grasses, the branches or the spikelets or both, as in orchard grass, grow toward one side of the axis on which they are borne. On the branches of the staminate inflorescence of teosinte, also, the spikelets grow toward one side.

Different stages in the development of the vegetative growing point and of the nascent inflorescence of orchard grass (*Dactylis glomerata* L.) are illustrated in figure 14, *A–H*.

A fully developed inflorescence is illustrated in figure 15.

The vegetative growing point of the grasses studied usually, if not always, soon becomes slightly compressed, but without any apparent distinction between the two faces. In orchard grass, even when the earliest secondary protuberances are forming (fig. 14, *C*), there are still few if any characters distinguishing the two sides. When, however, the tertiary protuberances begin to form (fig. 14, *D* and *E*) the primary shoot is already strongly bifacial. This becomes even more pronounced at later stages and extends to the shoots of the higher orders, finally constituting one of the characteristic features of the mature inflorescence. Thus the one-sided character of the spikelet clusters is initiated at about the time when the secondary protuberances of the rudimentary inflorescences begin to produce branch protuberances of higher orders.

Foxtail Millet

In the inflorescences of the foregoing species of grasses, each protuberance ultimately organizes a spikelet at its distal end. In foxtail millet, however, some of the protuberances of the higher orders elongate into sterile bristles (*28, p. 19*).

Various stages of the vegetative and reproductive phases of foxtail millet (*Setaria italica* (L.) Beauv.) are illustrated in figure 16, *A–M*.

The specimens illustrated in figure 16, *A–K*, are from shoots dissected in late September and early October. In the nascent inflorescence of figure 16, *B*, the irregularities in the primordia appear to be due to the initiation of protuberances. In the nascent inflorescence shown in figure 16, *C*, distal to the three phytomers crowned with leaf fundaments, there are very rudimentary reproductive phytomers without leaf fundaments. Two of these phytomers are initiating groups of three protuberances on their visible side. The central and uppermost protuberance of each group is situated in the same plane as the leaf apex of the basal phytomer.

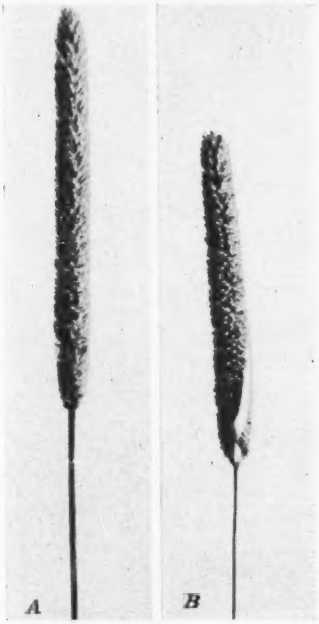

Figure 11.—Timothy: *A*, A typical inflorescence; *B*, an inflorescence in which the most proximal group of spikelets is subtended by a reduced leaf.

The positional relations of the members of each group are such as to suggest that the central one of the three is an incipient secondary shoot and that the other two are the first and second tertiaries at the base of its lateral flanks. This simultaneous initiation of the secondary shoot and its two lowest tertiaries, when taking place on the alternate sides of acropetally successive phytomers, would result in the appearance of protuberances in six longitudinal rows (fig. 16, *D*, *E*, and *F*), a condition characteristic of millet (*75*).

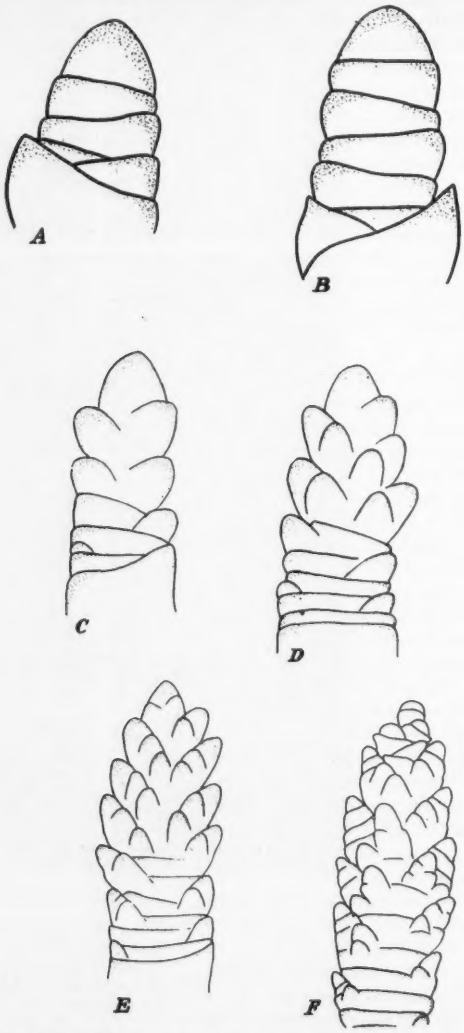

FIGURE 12.—Tall oatgrass. *A* and *B*, Vegetative growing points at different stages of development; *C*, nascent inflorescence; secondary protuberances are forming; *D*, the earliest tertiary protuberances are being organized on the lateral faces of the older secondaries, while additional secondary protuberances are continuing to develop acropetally and basipetally; *E*, additional tertiary protuberances have formed, and the glumes on the terminal spikelet have begun to develop; *F*, quaternary protuberances are developing on the flanks of some of the older tertiary branches. The terminal spikelet is more advanced and specialized than any of the lateral ones, protuberances representing florets having appeared in the axils of its two oldest lemmas.

With approaching cessation of apical elongation of the primary axis, the extremely short secondaries and tertiaries rapidly initiate groups of protuberances of higher orders (fig. 16, *G*), which later develop into groups of spikelets and bristles, disposed in six longitudinal rows (fig. 16, *H*), and in the mature inflorescence shown in figure 17.

In order to obtain more precise evidence concerning the stages shown in figure 16, *B* and *C*, studies were made in a later year of the growing points of vigorous plants that had been seeded in the open in early June. Strong shoots dissected in late July had formed a considerable number of rudimentary phytomers above the highest foliage leaf; secondary protuberances were being initiated in advance of their tertiaries. At the young stage shown in figure 16, *L*, the secondary protuberances were being initiated acropetally and basipetally from the middle region and the older ones were showing a decided extension of one flank. At the slightly older stage presented in figure 16, *M*, the primodria of two tertiary protuberances were visible on the flanks of each of the older secondaries.

Goebel (*28*) and others have classified the inflorescences of millet and certain other grasses as belonging to the "radial" type. These inflorescences were supposed to be polystichous instead of distichous as in most grasses. The observations on millet made in this study show that the apparently polystichous groups actually originate from secondary protuberances having a distichous and alternate arrangement, as such groups do in timothy. These results indicate that millet should go in Goebel's "falsely radial" type, along with *Alopecurus*, *Phleum*, etc., the inflorescences of which are actually distichous.

FIGURE 13.—Inflorescence of tall oatgrass.

TEOSINTE

In some grasses, as teosinte, the staminate and pistillate florets are in separate inflorescences, which have different forms. The pistillate inflorescence of teosinte (*Euchlaena mexicana*) has already been referred to under the description of once-branched inflorescences. The staminate inflorescence is multiple-branched, with elongated internodes; different stages in its development are illustrated in figure 18, *A–K*.

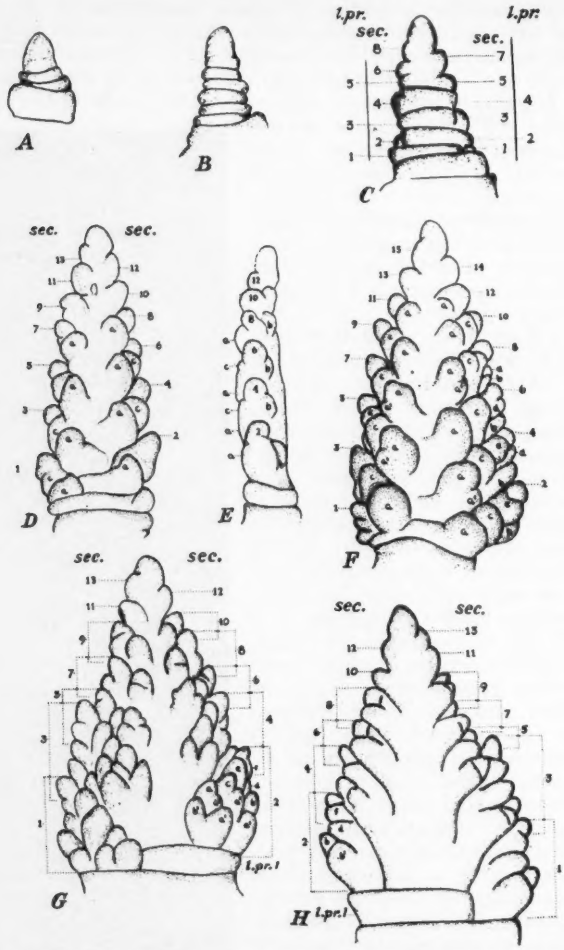

FIGURE 14.—Orchard grass. *A*, *B*, *C*, *D*, *F*, *G*, and *H*, viewed at right angles to the plane of the leaves and secondary protuberances; *E* in the plane of the secondaries. Leaf primordia (*l. pr.*) and secondary protuberances (*sec.*) are numbered from the base upward; *a*, *b*, *c*, etc., are successive tertiaries; *a'*, *b'*, *c'*, successive quaternaries; *A* and *B*, two vegetative growing points at different stages; *C*, a nascent inflorescence, soon after transition from vegetative phase; *D* and *E*, a face and an edge of a rudimentary inflorescence at the stage in which tertiary protuberances are forming on the secondaries; *F*, a slightly older inflorescence, the face of which corresponds with that of *D* and *G;* quaternary protuberances are just being initiated on some of the tertiaries; *G* and *H*, opposite faces of a still older rudimentary inflorescence, sometime before the branches had begun to elongate; the right side of *G* is the left of *H;* the organization of the foundational skeleton of the inflorescence is now nearly complete; each numbered bracket includes a secondary with the tertiaries and quaternaries arising from it.

The first indication of the transition from the vegetative to the reproductive phase and of the inception of the inflorescence is an especially vigorous growth of the apical meristem of the growing point, resulting in a relatively long, externally undifferentiated meristematic cylinder, slightly compressed in cross section and with a broadly rounded summit. Following or coincident with this first spurt of elongation, secondary protuberances begin to form at the base of the cylinder (fig. 18, *B* and *C*).

The process of initiation and development on the central axis of secondary protuberances and their tertiaries (*42*) continues in acropetal succession as shown in a much later stage in figure 18, *D* and *E*. This figure also illustrates the pronounced bifaciality of the primary shoot, which, together with the frequent tendency to droop in its mature condition, has caused it to be regarded as a secondary branch (*77*, *p. 320*). In this inflorescence the two proximal secondaries and their lowest tertiaries have developed into elongated lateral shoots, of which only the stumps are shown. Above these the secondaries and tertiaries have not elongated as branches. Instead, each secondary organized directly into a pediceled spikelet and is tertiary into a sessile spikelet. Similarly, the proximal elongated secondary shoots (fig. 18, *F–J*) organize their tertiaries into pediceled spikelets, their quaternaries into sessile ones. The elongated basal tertiary

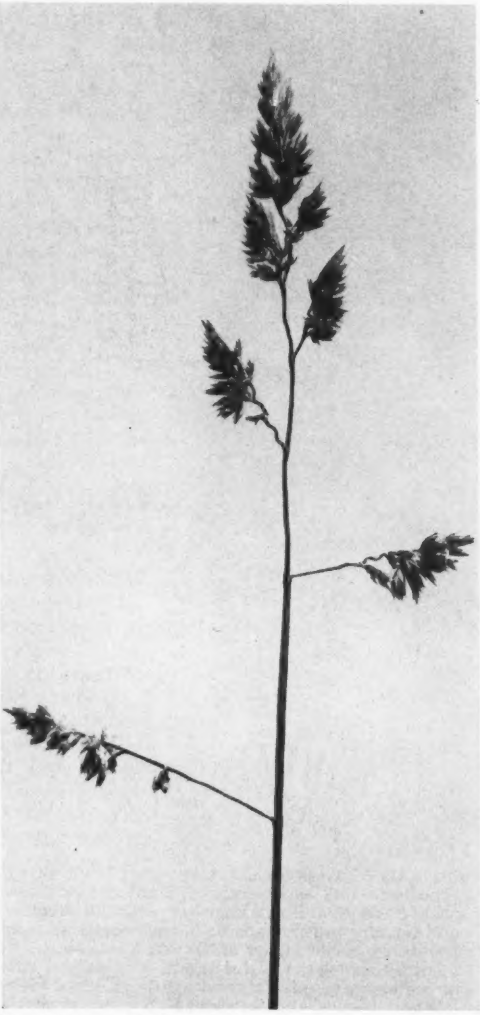

FIGURE 15.—Fully developed inflorescence of orchard grass.

shoots organize their quaternaries into pediceled spikelets, their quinaries into sessile ones.

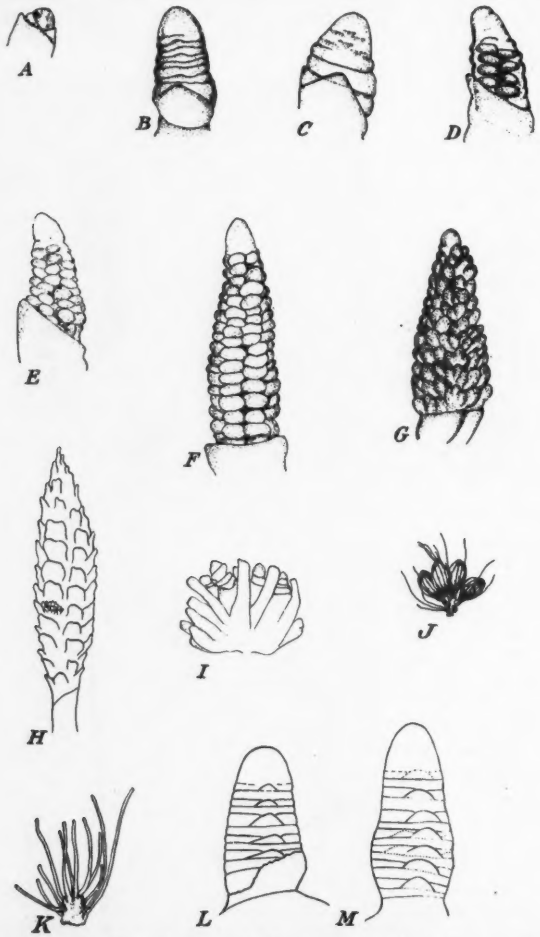

FIGURE 16.—Foxtail millet: *A*, A vegetative growing point; *B*, a nascent inflorescence at a very early stage; *C*, a nascent inflorescence, slightly more advanced than *B*; *D*, *E*, and *F*, somewhat older inflorescences with six rows of secondary and tertiary protuberances; *G*, each secondary and tertiary forming a group of protuberances of higher orders; *H*, a late stage of organization; groups of rudimentary spikelets and bristles in longitudinal rows; diagrammatic; *I*, a group of rudimentary spikelets and bristles, adaxial view; *J*, a group of mature spikelets and bristles, abaxial view; *K*, a group of bristles without spikelets, from the base of the inflorescence; *L* and *M*, nascent inflorescences of vigorous shoots; *L*, with secondary protuberances; *M*, tertiaries forming.

During the development of the rudimentary staminate inflorescence the tertiary shoots, originating from tissue at the extreme base of a secondary shoot, may be separated from the secondary by the expanding tissue of the primary axis. Very slight displacements of this kind occur in the inflorescence shown in figure 19, at secondaries 2, 4, and 5, and are shown diagrammatically in figure 18, *K*. In the panicles of some other grasses the most proximal tertiary shoots may also be displaced upward on the rachis for considerable distances above the secondary shoots from which they originated, in the manner described by Strasburger (*67, p. 118*).

A pistillate inflorescence with staminate spikelets in the distal part is illustrated in figure 20. The spikelets, each consisting of one floret with its silk (style and stigma), are arranged alternately in two ranks. This distichous arrangement is continued into the distal part of the inflorescence, where each phytomer gives rise to two staminate spikelets instead of a single pistillate spikelet.

FIGURE 17.—Mature inflorescence of foxtail millet.

LATER DEVELOPMENTS IN THE INFLORESCENCE IN RELATION TO PHYTOMER INITIATION

One might expect that spikelet and floret formation would progress in the same order as phytomer organization. Actually this is not the case. It has already been pointed out that in general the earliest secondary protuberances appear in the middle region of the incipient inflorescence and that new protuberances are successively formed distally and proximally to these. However, further development of spikelets and florets takes place more rapidly in the distal regions than in the middle and basal regions of the young inflorescence. The exact order and extent of this progress differs in detail with different species.

Corresponding with the more rapid specialization and sexualization of the most distal and youngest phytomers and with the early development of spikelets and florets in that region, flowering and maturing of seed also begin there (*21, figs. 1, 2; 32, p. 15; 76, p. 1062;*

84, p. 24). The way in which blooming begins near the apex and progresses more or less regularly toward the base of an inflorescence of the European species *Phalaris truncata* Guss. is illustrated in figure 21.

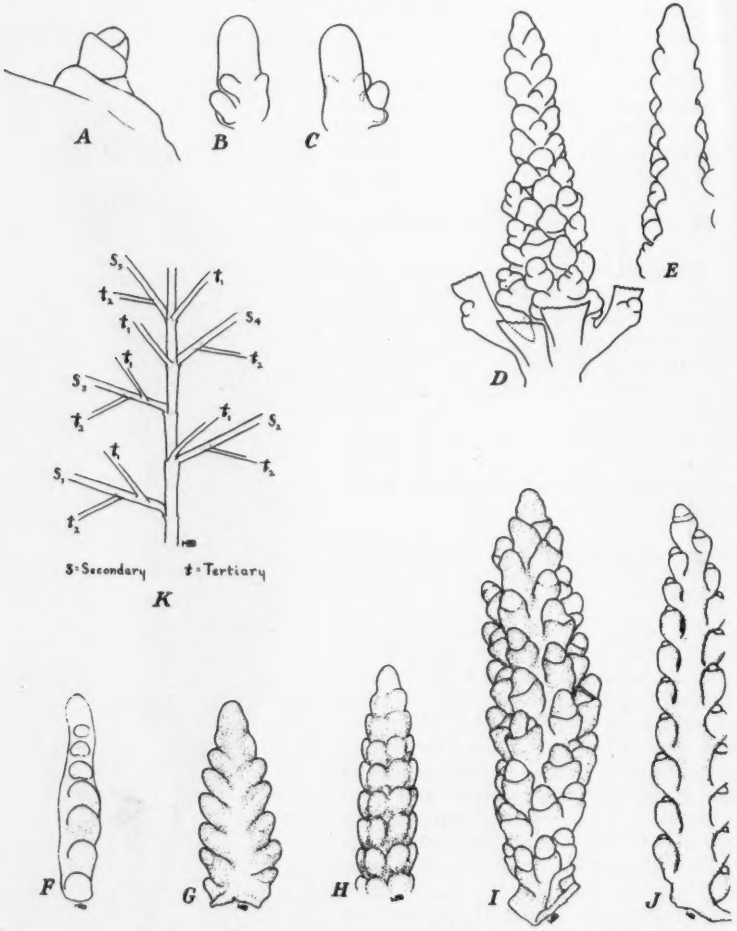

FIGURE 18.—Teosinte: *A*, A vegetative growing point; *B* and *C*, opposite faces of an inflorescence at its inception; *D* and *E*, opposite faces of the inflorescence at a considerably later stage of development; *F* and *G*, two views, edge and face, of a very young secondary shoot with tertiary protuberances, from the lower part of an inflorescence; *H*, an older secondary shoot with both tertiary and quarternary protuberances, abaxial view; *I*, an abaxial view of a secondary shoot at stage of spikelet organization; *J*, an adaxial view of another secondary shoot at about the same stage as *I*; *K*, skeletal diagram of the lower part of the inflorescence shown in figure 19.

That the last florets to bloom or the last seeds to mature in an inflorescence of grass are those at its extreme base may be partly

explained for many inflorescences by the fact that they originated from the phytomers which were the last to produce secondary protuberances. That this is not the complete explanation, however, is indicated by the fact that the most distal secondary protuberances originate later than those near the middle of the inflorescence, yet the florets near the apex may all be past bloom while in the middle region large numbers are still blooming (fig. 21).

In some grasses, e. g., timothy, the latter phenomenon may be explained in part by the fact that near the apex of the inflorescence the

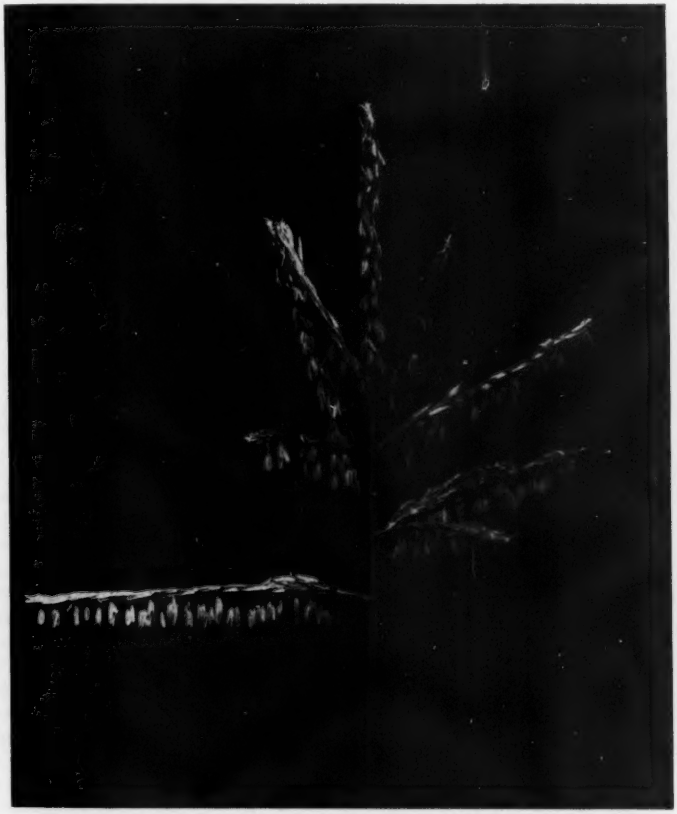

FIGURE 19.—Staminate inflorescence of teosinte.

secondary protuberances produce, through branching, relatively few protuberances of higher orders, while throughout the middle part of the inflorescence the protuberances continue for some time to subdivide and produce higher orders of branches and spikelets.

On the other hand, the relatively early flowering and early maturing of seed near the tip of the inflorescence may be due to the gradual acropetal diminution in the number and size of the vascular bundles of the axis, described by Dutailly (*20*), in 1873, and more recently

by Bugnon (*13*), in 1920, and Arber (*2*), in 1928. Or, more specifically, to a condition of the phloem in the bundles, resulting in a "natural girdling" as was suggested by Roberts and Wilton (*55*), in 1936, for dicotyledons.

DEVELOPMENT OF EITHER VEGETATIVE OR REPRODUCTIVE PARTS FROM THE SAME RUDIMENTARY PHYTOMER

To determine whether an individual rudimentary phytomer of a grass shoot remains for some time capable of either vegetative or reproductive development, depending upon the conditions for growth, timothy was grown under short and under long days.

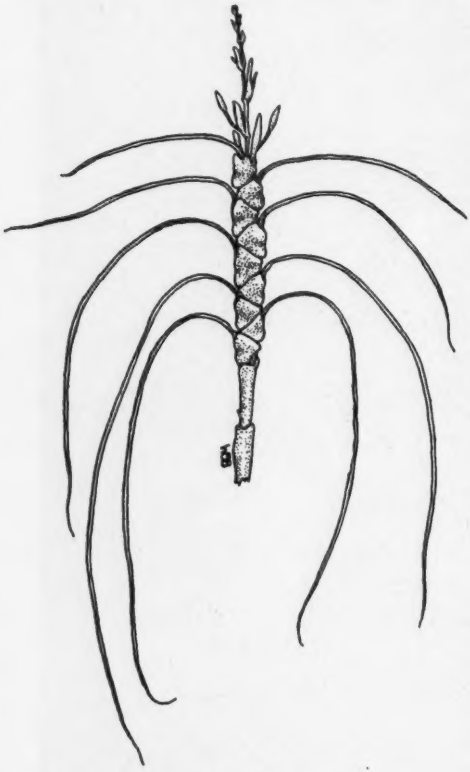

FIGURE 20.—Pistillate inflorescence, with staminate spikelets in distal parts of teosinte.

A number of plants were transferred from the field to the greenhouse on December 1, 1925. They grew under natural length of day until January 9, 1926, then with 7 hours' illumination each day until January 27, 1926. Each plant was then divided into two parts, one of which was grown under short-day, the other under long-day conditions, until March 10, 1926. The short-day plants were covered with a dark box from 4 p. m. until 9 a. m., and were thus illuminated for 7 hours each day. The long-day plants were illuminated artificially, from about sunset until midnight each day, by means of an ordinary 200-watt electric-light bulb suspended about 30 inches above the surface of the soil in which the plants were growing; they were thus illuminated for a total period of about 17 hours each day. All the plants continued to grow with natural illumination from March 10 to April 14.

For observation, shoots were selected that had started their development at approximately the same time, had produced the same number of leaves per shoot, and were therefore relatively uniform.

When the plants were first placed under artificially controlled lengths of day, the leaves were removed from several typical shoots and a count was made of the number of rudimentary phytomers in the growing point of each; there was an average of 14.75 rudimentary phytomers per growing plant.

Final records were obtained from four shoots grown under short days and from four shoots grown under long days.

Under short days, all shoots remained in a vegetative condition and the number of leaves continued to increase until the close of the experiment; an average of 8.5 new leaves per shoot developed from January 27 to April 14. Under long days during the same period, an average of 1.5 new leaves formed and on each shoot an inflorescence developed.

By subtracting the number of leaves that developed on the long-day plants from the number that developed on the short-day plants, it is evident that on an average seven phytomers in corresponding positions produced leaves under short days but under long days became a part of the inflorescence.

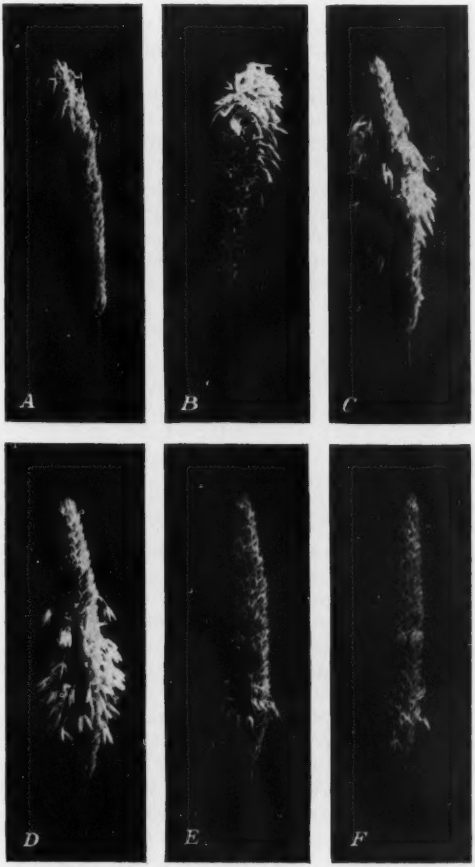

FIGURE 21.—Inflorescence of *Phalaris truncata* Guss. on different days during the blooming period: *A*, First day; *B*, second day; *C*, seventh day; *D*, ninth day; *E*, eleventh day; *F*, fifteenth day.

The results demonstrate quite conclusively that, for some time after the formation of a rudimentary phytomer in the growing point of a grass shoot, it remains capable of developing either vegetative or reproductive parts according to the conditions for growth.

THEORY IN REGARD TO DISTICHOUS ORIGIN OF PARTS OF INFLORESCENCE IN ALL GRASSES

In the representatives of the seven tribes of the grass family that have been studied during this investigation, it has been found that, notwithstanding the great variety of forms which the inflorescence

assumes in its fully developed state, its initiation is always marked by the formation of protuberances arranged distichously in the same plane as the leaves of the shoot. This fact seems to justify the conclusion that in all grasses the distichous arrangement of the leaves and of the primary branches on the vegetative part of the shoot is continued into the inflorescence without change in the sequence of homologous parts.

It is generally thought that in maize (*Zea mays* L.) the pistillate inflorescence, or ear, and also the central axis of the staminate inflorescence, or tassel, have a polystichous phyllotaxy (*28*; *81*, *p. 90*). Three or four theories have been advanced by different botanical writers and investigators as explanations of the way in which this polystichous arrangement originated (*16*; *78*, *pp. 110–113*). However, the investigations described herein indicate that it is probable that in maize, as in other grasses, the arrangement of the spikelets on the central axis is fundamentally distichous.

SUMMARY

A study was made of the vegetative growing point of eight species of grasses, belonging to seven tribes; of the morphological changes that take place in the growing point during its transition from the vegetative to the reproductive phase; and of the organization and early development of the inflorescence.

In the vegetative part of a grass shoot each internode, together with the leaf at its upper end and the bud or potential bud at its base, constitutes a phytomer. The young phytomers of the vegetative growing point are called rudimentary phytomers. Their leaf fundaments are at first slight transverse ridges, which quickly encircle the rudimentary axis.

The growing point is at first cone- or dome-shaped, slightly compressed, usually a fraction of a millimeter long, consisting of a very few (usually one to three) rudimentary phytomers below the undifferentiated apical meristem.

The apical meristem lays down the rudimentary phytomers, one after the other, in acropetal succession and at rather regular intervals of time; this constant period is known as the plastochrone.

There may be such a lag in leaf formation that the number of accumulated rudimentary phytomers gradually increases and the growing point assumes a cylindrical form. This occurs in such species as quackgrass, perennial ryegrass, timothy, and tall oatgrass.

In certain other species, e. g., in the staminate inflorescence of teosinte, only a slight accumulation of rudimentary phytomers occurs during the vegetative phase, but at the transition to the reproductive phase the apical meristem elongates very rapidly into an externally undifferentiated cylinder from which the greater part of the inflorescence develops.

One of the earliest indications of the inception of an inflorescence is the appearance of swellings or protuberances. In many grasses they arise at about the middle region of the growing point, usually with a distichous arrangement, and continue to form for some time in both acropetal and basipetal succession. In the basal or proximal part of the inflorescence, each protuberance is in the axil of a ridge or leaf primordium; in the apical or distal part, they form without subtending ridges. These secondary protuberances have the same relative posi-

tion on the primary axis as the vegetative buds and are their homologues.

In some grasses, such as quackgrass, perennial ryegrass, and others, the secondary protuberances do not give rise to protuberances of higher orders. In many other grasses, such as timothy and orchard grass, the secondary protuberances do give rise to protuberances of successively higher orders.

In some grasses, such as foxtail millet, the primary branches, that is, the secondary shoots, of the inflorescence seem to arise polystichously. However, evidence obtained in this investigation indicates that fundamentally the secondary shoots of inflorescences of this type originate distichously, as in other grasses.

Environmental conditions largely determine whether vegetative or reproductive development takes place. For many grasses, length of day is one of the most important of these conditions. In timothy, under short days, all of the rudimentary phytomers developed vegetatively; under long days, from rudimentary phytomers in corresponding positions on the growing points, reproductive development occurred.

As a rule, each protuberance, whatever its order, ultimately organizes a spikelet at its apex. There is a general tendency for spikelet formation to begin in the upper middle region of the young inflorescence and to progress both acropetally and basipetally. Further specialization, however, is more rapid in the distal region than in the middle and proximal regions. Consequently, flowering and seed maturation progress from the apex toward the base of the inflorescence, in the reverse order to phytomer formation.

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A COMPARATIVE STUDY OF THE SEASONAL ROOT DEVELOPMENT OF SOME INBRED LINES AND HYBRIDS OF MAIZE [1]

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INTRODUCTION

In an endeavor to gain further knowledge of the root system of corn (*Zea mays* L.), an investigation was planned to include both the developmental and genetic aspects. Some of the primary objectives were as follows: (1) To obtain a detailed record of the growth of the root system of corn from planting to maturity; (2) to determine the range in root characters among certain inbred lines; (3) to ascertain how these root characters are expressed in hybrid combinations; and (4) to identify any characters possibly associated with the force required to pull a corn plant from the ground.

HISTORICAL REVIEW

Pavlychenko (*16*)[3] recently published an excellent review of the various methods employed in the past in the study of root systems. In addition to his own "soil-block" washing method, he described 11 different procedures used by previous investigators, viz, direct washing, trench washing, steel-frame washing, soil-prism washing, concrete-compartment washing, nail-and-needle-brush washing, Hellriegel's steel cylinder, water-culture and soil containers, observation pit, direct tracing, and Weaver's trench method. Sayre [4] used the "lithium" method to determine the extent of corn root systems. After lithium had been placed in the soil at definite distances from the plant, the stalk was tested for its presence. By this means he hoped to determine the lateral extension of the root system. The results, however, failed to agree with observations made by the direct tracing of the roots. Sayre suggested that his results may more nearly represent the absorptive area of the corn root system than the maximum extension of some of the individual roots.

The majority of the investigations relating to the roots of corn have been primarily concerned with the distribution of the roots in the soil. The reports vary widely as to the extension of the root system vertically and horizontally. Hickman (*7*), in Pennsylvania, and Farris (*3*), in New Jersey, found that the root system was relatively shallow. The maximum distance of penetration in New Jersey was only 2 feet,

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[3] Italic numbers in parentheses refer to Literature Cited, p. 537.

[4] SAYRE, J. D. THE LITHIUM METHOD OF MEASURING THE EXTENT OF CORN ROOT SYSTEMS. 1937 [Unpublished.]

both laterally and vertically. Other reports on the distribution of the roots of corn have come from Morrow and Hunt (*15*), in Illinois, Hays (*6*), in Minnesota, King (*11*), in Wisconsin, Ten Eyck (*24, pp. 333–346; 25*), in North Dakota and Kansas, Shepperd (*20, pp. 529–535*), in North Dakota, Miller (*14*), in Kansas, and Weaver et al. (*26, 27*), in Nebraska. This group of investigators found corn roots at depths ranging from 4 to 8 feet and with lateral extensions ranging from 2 to 4 feet. In all cases the corn root system extended to considerably greater distances than those reported from Pennsylvania and New Jersey. Several of these workers noted that the crown roots from the lower nodes extended almost horizontally from the culm, whereas the roots from the higher nodes often extended nearly vertically into the soil.

Less attention has been devoted to the seasonal development of the root system of corn than to the distribution in the soil of the roots of a mature plant. Hickman (*7*) obtained measurements of the size of the root systems at 2, 4, 6, and 8 weeks after planting. In general, his observations during this period of growth agree with those in the present study. Weihing (*28*) examined corn roots 2, 4, 6, 8, and 12 weeks after planting, both in pots and in the field. Rotmistrov (*18*) found that from the "bushing" to the flowering period maize roots averaged a daily growth of 1.5 cm. vertically and 0.8 cm. horizontally. Bensin (*1*), in Czechoslovakia, observed that the maximum extension of the roots was reached at the time of tasseling.

In connection with the lodging of corn, the study of the root system has naturally assumed some importance. Holbert and Koehler (*8*) designed a plant-pulling machine to determine the force required to pull a plant from the ground. Koehler, Dungan, and Holbert (*12*) observed that an inbred strain of corn with the ability to stand erect possessed a root system about twice as large as that of a strain inclined to lodge. Hayes and McClelland (*5*) found that—

> * * * where parents (inbred lines) were widely different in ability to withstand lodging, the F_1 was, in general, of intermediate habit, although there were some exceptions to this rule. When both parents had low lodging indices, the F_1 crosses were also low and when both parents had high lodging indices, the F_1 crosses lodged severely, as a rule.

Wilson (*30*) noted that the presence of many brace roots and short distances between the lower nodes of the corn plant were important in the prevention of lodging. Pettinger (*17*) found that potassium and phosphorus were especially beneficial in promoting strong root growth. The weather, however, was found to be a more important factor in the determination of lodging than either the fertilizers or the cropping systems employed. Hall (*4, p. 26*) observed that lodging was determined by a complex of morphological factors and—

> * * * that strong lines were strong because they possessed one or more characters that correlate highly with erect plants and in spite of the fact that they also possessed certain characters that might be associated with weak lines.

Literature relating to purely genetical studies of root characters is scarce. The only gene definitely identified in connection with a root character of corn has been described by Jenkins (*9*). Plants exhibiting the effects of this gene have fewer primary (or main) roots than has ordinary corn. Kiesselbach and Weihing (*10*), studying mature plants, noted the comparative root development of selfed lines of corn

and their F_1 and F_2 hybrids. Hybridization markedly stimulated the penetration, spread, length, and diameter of the roots in the first generation, whereas those of the second generation were intermediate in these respects. Smith (*23*) noted that a high ratio of secondary roots to primary roots was the rule in "phosphate efficient" lines and that in the F_1 a high ratio of secondary to primary roots was dominant over a low ratio.

Some attention has been given to the seminal root system of corn. Wiggans (*29*) reported that dent corn and popcorn usually have four "temporary" roots (including the radicle). Flint and sweet corns usually have only one temporary root, the radicle. Siemens' (*21*) results were similar to those of Wiggans, except that he found Michigan popcorn among those types that have no secondary seminal roots. Smith and Walworth (*22*) believed they had accumulated rather strong evidence for a significant positive correlation between yield and seminal root development, but Collins (*2*) advanced certain criticisms against their methods. Mangelsdorf and Goodsell (*13*) failed to find a correlation between seminal root development and yield in four out of five tests.

MATERIALS AND METHODS

The strains selected for the root studies consisted of four inbred lines, 56, 4–8, 51, and 84; two single-cross hybrids, 56 × 4–8 and 51 × 84; and one double-cross hybrid, (56 × 4–8) × (51 × 84). The four inbred lines are at present being widely used in Ohio in the commercial production of hybrid seed corn. Line 56 matures at about the average date at Wooster, Ohio, line 4–8 later than average, and lines 51 and 84 approximately 10 days earlier than average.

The planting was made in the spring of 1937 at the Ohio Agricultural Experiment Station at Wooster as part of the regular farm rotation of corn–oats–wheat–alfalfa. The soil type, Wooster silt loam, is derived from sandstone and shale, glaciated, and naturally well drained.

The average monthly precipitation and temperature during the 1937 season at Wooster closely approximated the 40-year average.

The planting was arranged in four replications of three-row plots. The individual plants were separated by a minimum distance of 40 inches.

The planting was made on May 27, and the first root samples were obtained 16 days later. The samples consisted of five root systems of each strain, and they were taken at random on the same day of each succeeding week until 15 weeks after planting. The root systems were removed from the ground in a cylinder of soil 16 inches in diameter and 10 inches in depth, securely wrapped with burlap, and thoroughly soaked prior to removal of the soil with a fine spray of water. Practically no rootlets were lost by this washing process. Obviously, a cylinder of soil of these dimensions did not include the entire root system, but direct tracings of the roots by the trench method indicated that the great bulk of the root system, including practically all of the fibrous portions, was obtained.

Direct tracing of the crown roots, by the trench method, was accomplished for one plant of each strain at three times during the season.

THE SEMINAL ROOT SYSTEM

DRY WEIGHT, COMBINED LENGTH, AND NUMBER OF SEMINAL ROOTS

Table 1 gives the mean values obtained for the measurements of the seminal roots of the inbred lines and hybrids from the second to the seventh week after planting. The dry weights of the roots of the inbred lines reached a maximum at about the fourth week and those of the hybrids at about the fifth week, after which time their dry weights decreased. At 3 weeks, the first internode of many of the plants began to show severe rot injury. With the partial or complete death of the tissues in this region, it is doubtful whether the seminal root system was any longer active in absorption. At least 5 weeks before the crown root systems reached their maximum growth, the seminal root systems were entirely dead. It is believed that this premature death of the seminal roots was due entirely to the many injurious insects and fungi present in the field soil.

TABLE 1.—*Average weight, length, and number of seminal roots per plant in the inbred lines and hybrids from the second to the seventh week after planting*

Inbred line or hybrid	Average values for seminal roots per plant from the second to the seventh week after planting		
	Dry weight	Total length	Roots [1]
Inbred lines:	*Gram*	*Centimeters*	*Number*
56	0.062	53.3	3.9
4-8	.080	46.4	4.0
51	.085	45.5	3.4
84	.053	45.9	3.8
Minimum significant difference [2]	.020	12.4	.37
Hybrids:			
56 × 4-8	.143	73.7	4.7
51 × 84	.133	64.0	4.3
(56 × 4-8) × (51 × 84)	.155	67.9	4.3
Minimum significant difference [2]	.038	10.9	.41

[1] Including the radicle.
[2] Minimum difference for significance calculated as twice the standard error of a difference.

Even 16 days after planting, the seminal roots of the hybrids exhibited marked hybrid vigor, in contrast to the roots of the inbred lines. This was apparent in the fact that the hybrids had a greater number of roots, with a greater dry weight and combined length. The hybrids showed significant differences only in respect to number of roots, whereas the inbred lines showed significant differences in number and dry weight (table 1). Consequently, the differences between the seminal roots of the inbred lines were reflected between the hybrids only in respect to the number of roots.

It was of interest to note in what degree the seminal root development of the various strains correlated with the development of the crown roots and the shoot. Within neither group of strains was it possible to predict the relative number of crown roots from the number of seminal roots, nor was it possible to predict the relative dry weight of the crown roots from the dry weight of the seminal roots. Likewise, the information on the number or the dry weight of the

seminal roots did not permit a reliable estimate of the potentialities for development of the top of the plant or the yield of grain.

DISTRIBUTION OF SEMINAL ROOTS IN THE SOIL

The direct tracing study by the trench method at 30 days after planting indicated a predominantly horizontal distribution of both the radicle and the secondary seminal roots. Maximum distances of penetration observed for the radicle were 4 inches vertically and 7 inches horizontally. The secondary seminal roots occupied a position similar to that of the radicle.

THE CROWN ROOT SYSTEM

COMPARATIVE DEVELOPMENT OF CROWN AND SEMINAL ROOTS

The crown roots began a rapid growth soon after germination and in a short time far surpassed the seminal roots in dry weight. At 3 weeks after planting, the crown and seminal roots were about equal in dry weight. At only 6 weeks after planting, the crown roots were at least 25 times as heavy as the seminal roots, and for one strain the ratio was as great as 55 to 1.

DRY WEIGHT OF CROWN ROOTS DURING THE GROWING SEASON

The increase in the dry weight of the crown roots of both the inbred lines and the hybrids is illustrated graphically in figure 1, *A*. The data form a typical S-shaped growth curve. Distinct differences in dry weight could be observed at 16 days after planting, and at 15 weeks most of the strains were widely separated. When fully developed the largest root system (56 × 4–8) was twice the dry weight of the root system of the largest inbred line (4–8) and four times that of the root system of the smallest inbred line (51). The ratio of the dry weights of the roots between the two groups of strains, however, remained at a value of about 2 or 3 during most of the season.

The maximum dry weight of the crown roots was attained at approximately the time of silking for the majority of the strains. There was some indication that the maximum dry weight was attained the week following silking for two of the strains. Larger samples of each strain would be required to ascertain this point with greater accuracy.

The maximum dry weight of roots attained by a particular inbred line was related in some degree to its time of maturity. For example, line 4–8 was the latest of the lines to mature and had the greatest dry weight of roots. Line 51 was the earliest and had the least dry weight of roots. Line 84, however, was nearly as early as line 51 but had a considerably greater dry weight of roots. It would, therefore, seem that at least among the inbred lines certain hereditary factors other than time of maturity influenced the maximum dry weight of the crown roots. Among the hybrids the maximum dry weight of roots increased in the order of the lateness of maturity of the strains.

Differences in dry weight of roots among the inbred lines were reflected in the differences among the hybrids. The double-cross hybrid had a root weight somewhat intermediate between the single-cross hybrids, but, as in many other root characters, it most nearly resembled the single cross 56 × 4–8.

A differential seasonal response seems to occur among the four inbred lines, as indicated by the dry weights of roots at 10 weeks and 13 weeks after planting (fig. 1, *B*). On this basis lines 84 and 4–8 should resist lodging best, followed by lines 56 and 51. At 13 weeks

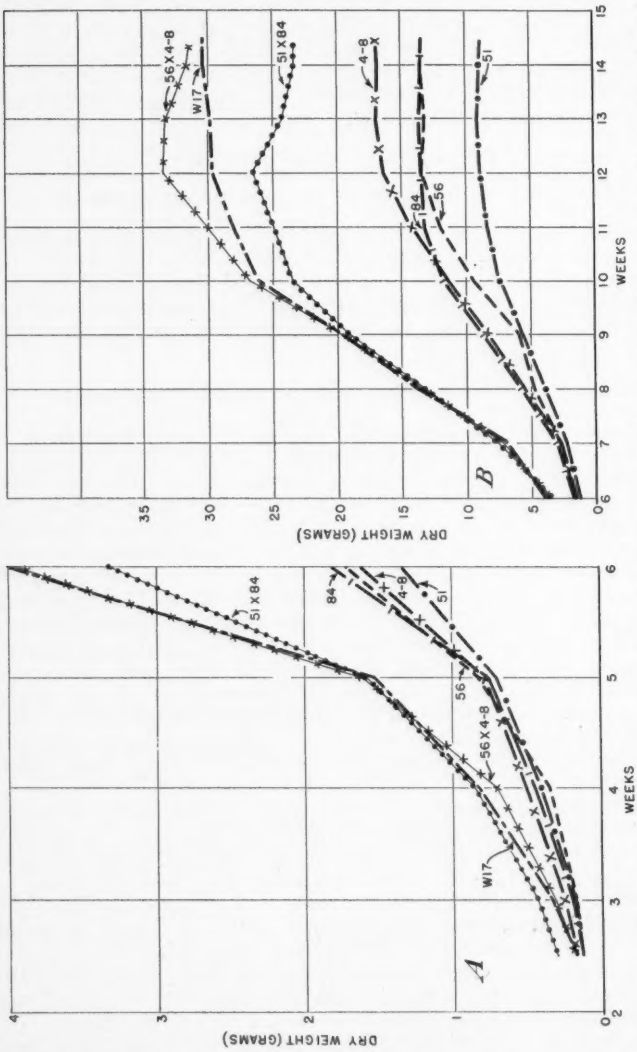

FIGURE 1.—Dry weight of the crown roots of inbred lines and hybrids from (*A*) the second to the sixth week and (*B*) from the sixth to the fifteenth week after planting. W17 is the double-cross hybrid $(56 \times 4\text{–}8) \times (51 \times 84)$. Curves smoothed by computing a moving average of 3 weeks' data.

after planting the expected order would be: 4–8, 56, 84, and 51. No data are available to test the differential seasonal root development as a criterion of the ability of a plant to resist lodging, but the problem is of sufficient importance to deserve further study. An examination

of the growth curves of the dry weights of roots of the hybrids shows that they differed little in dry weight up to 9 weeks after planting but that the differences increased after that time. Consequently, the possibility of a differential seasonal response with respect to lodging is likewise suggested for the hybrids.

TOTAL LENGTH OF MAIN ROOTS OF CROWN ROOT SYSTEMS DURING THE GROWING SEASON

The seven strains of corn differed in several root characters in addition to dry weight. Table 2 gives the mean total length of the main roots of the crown root systems for two different periods during the growing season. Obviously, the hybrids had a considerably greater total length of main roots than did the inbred lines. Within each group of strains, the differences are not so pronounced as they were in regard to dry weight. Line 51, for example, is the only one of the inbred lines differing significantly from the other lines in the total length of the main roots of the mature root systems. The total length of the main roots of the hybrids reflects a situation closely resembling that for dry weight of roots. The single crosses differed significantly in total length of the main roots of the mature root systems, but the double-cross hybrid differed significantly only from cross 51 × 84.

TABLE 2.—*Mean total length in centimeters per plant of the main roots of the crown root systems for the inbred lines and hybrids during two different periods of the growing season*

Inbred line or hybrid	Mean total length per plant of main roots of crown root systems for period indicated	
	Second to ninth week, inclusive	Eleventh to fifteenth week, inclusive [1]
Inbred lines:	*Centimeters*	*Centimeters*
56	395.0	931.5
4–8	384.7	894.7
51	292.8	528.9
84	379.6	932.5
Minimum significant difference [2]	59.96	69.19
Hybrids:		
56 × 4–8	528.4	1,239.0
51 × 84	479.9	1,051.3
(56 × 4–8) × (51 × 84)	470.3	1,200.5
Minimum significant difference [2]	55.60	146.85

[1] Beginning with the tenth week, length measurements were not taken on the roots of the lower three nodes because of the injury which they suffered from insects and root rots.
[2] Minimum difference for significance calculated as twice the standard error of a difference.

NUMBER OF "FUNCTIONAL" MAIN ROOTS DURING THE GROWING SEASON

Roots which entered the soil were arbitrarily termed "functional." The root systems of the hybrids exceeded those of the inbred lines by a considerable margin both in dry weight and total length of the main roots, but this was not true with respect to the number of functional main roots (fig. 2). For this latter character, the root system of one inbred line (4–8), when fully developed, exceeded that of any of the hybrids. The root systems of the hybrids, however, had more main roots than the remaining inbred lines. The hybrids

showed only small differences in this character, but again 56 × 4–8 and the double-cross hybrid were more nearly alike than were 51 × 84 and the double cross. Each single cross more nearly resembled the inbred parent having the larger number of main roots than it did the inbred parent having the smaller number of main roots.

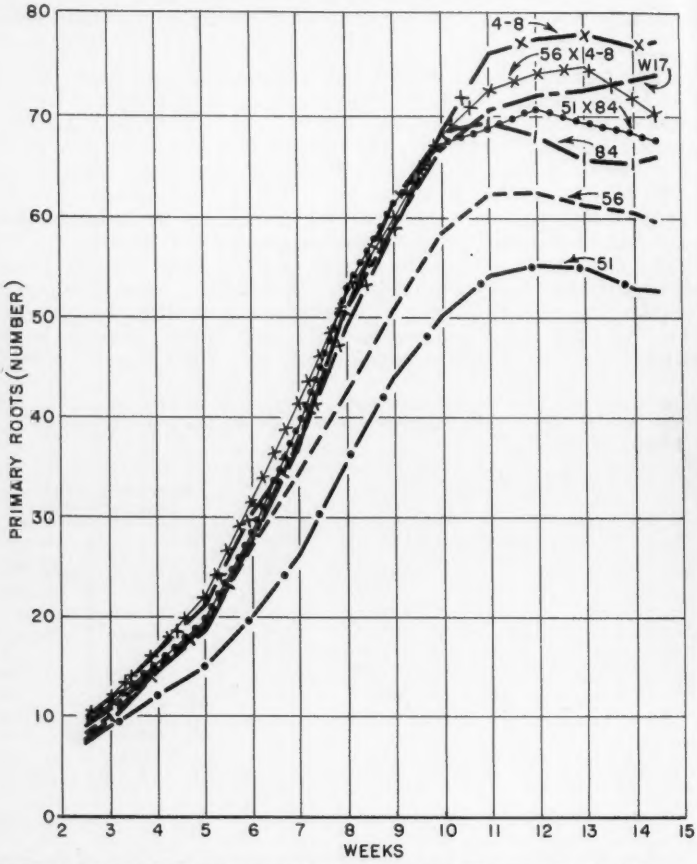

FIGURE 2.—Number of main roots in the crown root systems of inbred lines and hybrids of maize from the second to the fifteenth week after planting. W17 is the double-cross hybrid (56 × 4–8) × (51 × 84). Curves smoothed by computing a moving average of 3 weeks' data.

Differences in the number of functional main roots were evident at 16 days after planting and remained fairly consistent during the growing season. The mean number of main roots among all the strains ranged from 5.5 to 7.7 at 16 days and from 50.0 to 79.2 at 15 weeks. This root character, like dry weight and total length of main roots, reached a maximum value at or slightly subsequent to the time of silking.

ROOT DEVELOPMENT AT DIFFERENT NODES

CHARACTERISTICS OF CROWN ROOTS AT EACH NODE

The crown root system of corn develops by successively higher whorls of roots at closely set nodes. Theoretically, the scutellar node is the lowest node of the plant, but for practical purposes, the lowest node that gave rise to a whorl of crown roots was designated as the first node in this study. Successively higher nodes with whorls of crown roots were numbered in the order of their occurrence. Despite the proximity of these lower nodes, they are nearly always distinguishable, and rarely is any difficulty encountered in determining their exact sequence. The number of main roots per node increases rather slowly upward to the third or fourth node and then more rapidly at the nodes higher on the culm. A typical sequence of number of main roots for a mature plant of 56 × 4–8 from the first to the tenth node was as follows: 4, 4, 4, 4, 5, 7, 9, 12, 16, 13.

FIGURE 3.—Root systems of inbred lines and hybrids of maize 2 weeks after planting: *a*, Line 56; *b*, line 4–8; *c*, line 51; *d*, line 84; *e*, single-cross hybrid 56 × 4–8; *f*, single-cross hybrid 51 × 84; *g*, double-cross hybrid (56 × 4–8) × (51 × 84).

The main roots arising from the first three or four nodes were of a relatively small and uniform diameter throughout their length (fig. 3). These roots early develop an extensive growth of fine lateral rootlets. As the main roots from each higher node appear, there is a progressive increase in diameter, but this thickness is not maintained throughout their length. The earliest and most vigorous growth of lateral rootlets occurs proximally unless the main root sustains severe injury from some source. In that event, dependent upon the strain of corn concerned, the most vigorous growth of lateral rootlets may occur just proximal to the point of injury.

Probably one of the most significant facts revealed in this root study is that strains of corn differ tremendously both in the ordinary production of lateral rootlets and in their production subsequent to the severance of the main root by some insect pests. Two of the in-

bred lines employed in this study, 4–8 and 51, had a small number of lateral rootlets and the other two lines, 56 and 84, were plentifully supplied with them. These differences are readily seen in figure 4. Such variations in root growth must mean very great differences in

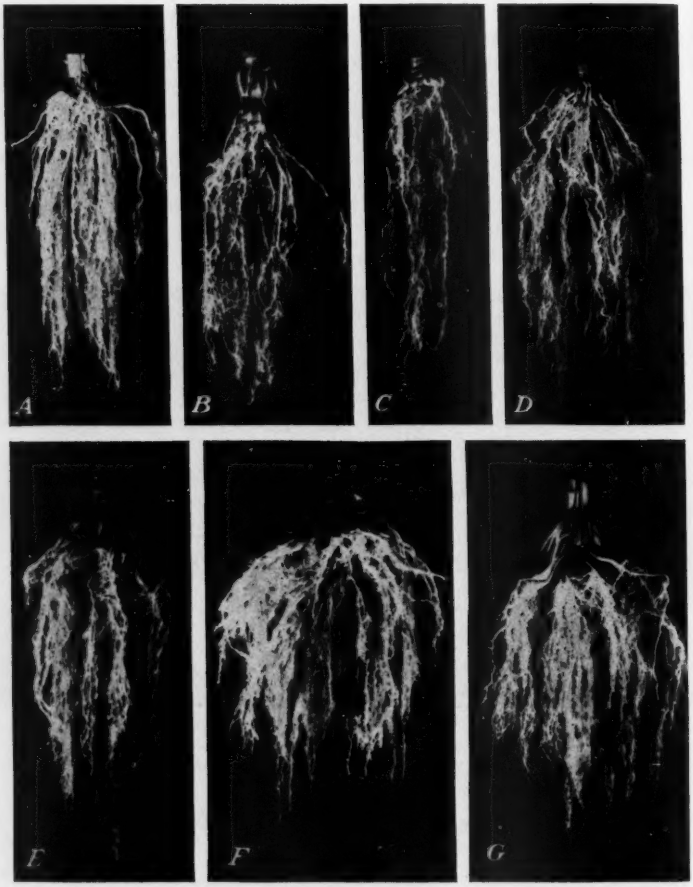

FIGURE 4.—Root systems of inbred lines and hybrids of maize 11 weeks after planting: *a*, Line 56; *b*, line 4–8; *c*, line 51; *d*, line 84; *e*, single-cross hybrid 56 × 4–8; *f*, single-cross hybrid 51 × 84; *g*, double-cross hybrid (56 × 4–8) × (51 × 84).

the total area of root surface in contact with soil particles, and, consequently, may be an important factor in soil, air, water, and nutrient relationships with the plant. The fact that the inbred lines show a differential response in lateral root growth following insect injury may be of importance in areas where corn is damaged as a result of the activities of such insect pests as the southern corn rootworm.

NUMBER OF WHORLS OF "FUNCTIONAL" CROWN ROOTS DURING THE GROWING SEASON

At 16 days after planting the number of whorls of crown roots (fig. 5) ranged from 1.7 to 2.0, and at 15 weeks after planting they

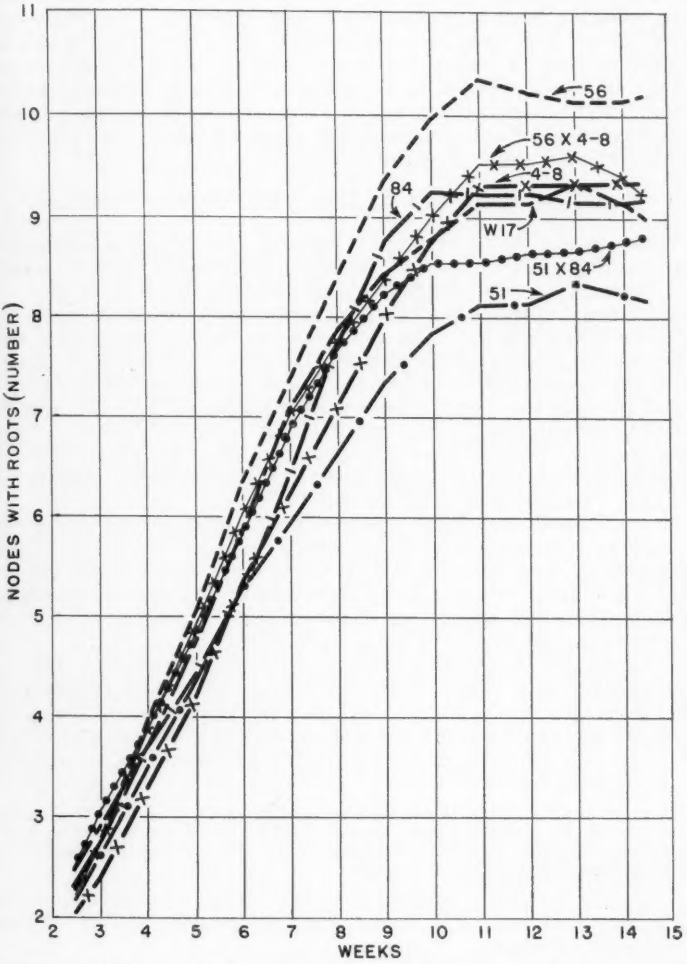

FIGURE 5.—Number of nodes per plant with main roots from the second to the fifteenth week after planting. W17 is the double-cross hybrid (56 × 4–8) × (51 × 84). Curves smoothed by computing a moving average of 3 weeks' data.

ranged from 8.0 to 10.4. In general, during the 1937 season about one additional whorl of roots developed each week for the first 8 or 9 weeks after planting.

In total number of nodes with roots, one of the inbred lines (56) again exceeded any of the hybrids. The fully developed root system of this line had slightly more than 10 nodes with roots, whereas the most poorly developed inbred line (51) had only 8 nodes. The single-cross hybrids exhibited a significant difference of nearly 1 whole node with roots in their fully developed root systems. One single-cross hybrid (56 × 4–8) most closely resembled the inbred line 4–8 with the smaller number of nodes with roots, whereas the other single-cross hybrid (51 × 84) seemed to be about intermediate to its component inbred lines in this root character. The single-cross 56 × 4–8 and the double-cross hybrid failed to differ significantly in the maximum number of nodes with roots.

TOP-TO-ROOT RATIOS DURING THE GROWING SEASON

At 16 days after planting, the top was one to two times heavier than the root system (fig. 6). Throughout the season this disproportion between the dry weights became constantly greater until 15 weeks after planting, when the top-to-root ratio was more than 20:1 for some of the strains. The ratios for the single-cross hybrids were approximately intermediate between the ratios of their inbred parents up to the time of silking, when the hybrid ratios tended to equal or exceed those of the inbred parent with the larger ratio. The double-cross hybrid exhibited a higher ratio than either of the single-cross hybrids up to 9 weeks after planting. Its ratio then became intermediate between the two single-cross ratios and finally appeared to be nearly identical with that of cross 56 × 4–8.

Several investigators have reported on the top-to-root ratio of corn at various periods during the growing season. Hickman (*7*), in Pennsylvania, found the ratio to be 0.6:1 for plants 2 weeks old and 3.2:1 for plants 4 weeks old. The corresponding average values for the hybrids in this study were 1.4:1 and 2.7:1. King (*11, Rpt. 9*), in Wisconsin, reported the ratio at maturity to be 6.7:1. Miller (*14*), in Kansas, found the ratio at maturity to average 9.6:1 in 1914 and 7.8:1 in 1915. Schweitzer (*19*), in Missouri, reported the ratio to be 23.7:1 on September 10. Weihing (*28*), in Nebraska, found the ratio to be 6.4:1 for a small variety grown to maturity in pots. Rotmistrov (*18, p. 51*) reduced the relationship to a general law by stating that—

> * * * at the beginning of the development the weight of the roots exceeds the weight of the superficial parts, in the middle part of the development, the relation approximates 1:1, and at the end of the development the weight of the superficial parts exceeds that of the roots.

This law did not seem applicable to the strains of corn included in this study, since even at 2 weeks after planting the top in all cases outweighed the roots.

In general, the top-to-root ratios of the strains in this study exceeded the ratios reported in previous studies. At 15 weeks after planting, the smallest ratio was 12:1 and the largest 23:1.

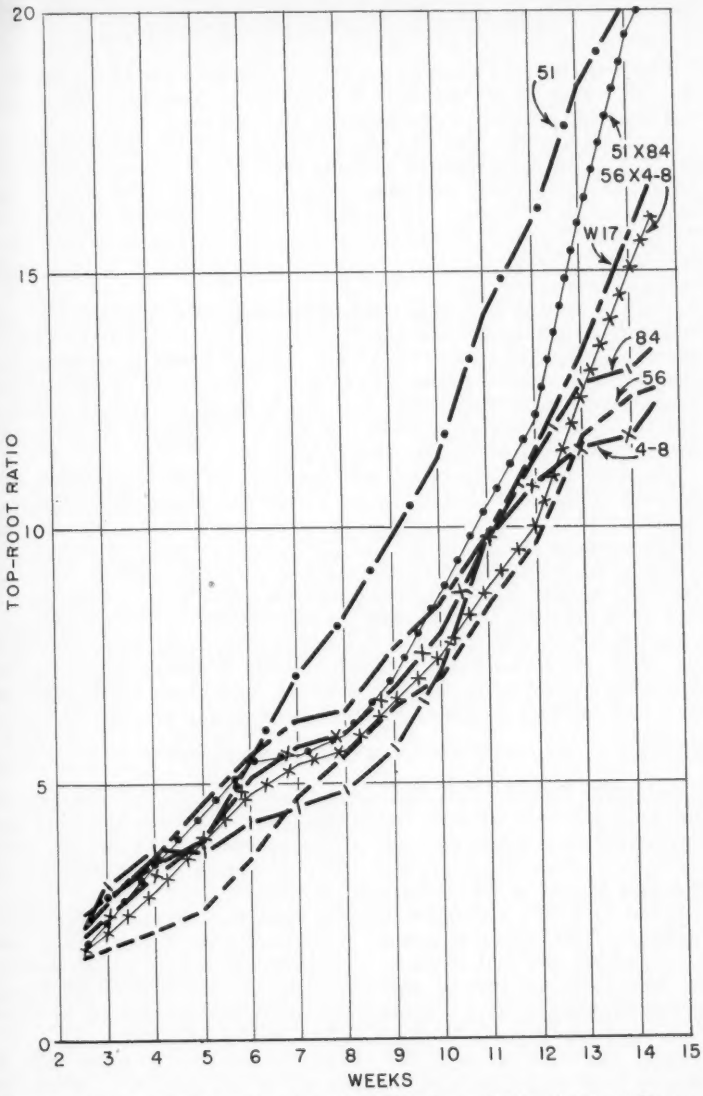

FIGURE 6.—Top-to-root ratios, based on the dry weights, of inbred lines and hybrids of maize from the second to the fifteenth week after planting. W17 is the double-cross hybrid (56 × 4–8) × (51 × 84). Curves smoothed by computing a moving average of 3 weeks' data.

DISTRIBUTION OF MAIN ROOTS OF CROWN ROOT SYSTEMS IN THE SOIL DURING THE GROWING SEASON

The main roots of the crown root systems were traced for one plant of each strain at 30, 49, and 87 days after planting. The trench method was employed in making the excavations.

At 30 days after planting, the main roots of the inbred lines had not quite penetrated halfway through the 7 to 12 inches of surface soil. Both the crown roots and the seminal roots extended nearly horizontally from the culm. The maximum lateral spread observed was 12 inches. No marked difference was evident between the inbred lines and the hybrids at this period either in the depth of penetration or in the lateral spread.

At 49 days after planting, most of the roots of the inbred lines had penetrated to a maximum depth of 10 to 12 inches and extended laterally to slightly greater distances. Line 51 had a root system that was markedly restricted in distribution. The roots of the hybrids seemed to be somewhat more extensively distributed at this period than the roots of the inbred lines. Maximum distances of penetration were 2 feet both horizontally and vertically.

The last examination of the root systems was made 87 days after planting. There seemed to be no significant changes in maximum values for the depth and lateral extension of the main roots since the 49-day examination.

It is apparent that the root system of corn extended to relatively short distances at Wooster during the 1937 season. The results agree with those obtained by Hickman (*7*), in Pennsylvania, and Farris (*3*), in New Jersey. The studies of King (*11*), Shepperd (*20*), Miller (*14*), and Weaver (*26*), in Wisconsin, North Dakota, Kansas, and Nebraska, respectively, indicate, however, that under certain soil and climatic conditions corn may be much more deeply rooted.

PULLING RESISTANCE AND SOME ASSOCIATED ROOT CHARACTERS

A plant-pulling machine was used to determine the force required to pull a single root system from the ground. This machine was equipped with a single movable pulley operating between the scales and a stalk attachment device.[5] Twenty plants of each strain were pulled on August 14, 11 weeks after planting.

All the hybrids surpassed the inbred lines in mean pulling resistance (table 3). The pulling resistance of the lines ranged from 158 pounds to 227 pounds and that of the hybrids from 290 pounds to 350 pounds. The low value for line 51 was expected on the basis of its poorly developed root system. The double-cross hybrid was nearly identical with the single-cross hybrid 56 × 4–8 in pulling resistance.

Mean values for some of the characters that might have been influential in promoting strong rooting are given in table 3. Correlation coefficients were calculated within strains between (1) pulling resistance and dry weight of the crown root system and (2) pulling resistance and the number of main roots (table 4). Significant positive correlations within five strains were found between pulling resistance and root weight. No significant correlations were evident between pulling resistance and number of main roots.

[5] Designed by A. A. Bryan, Division of Cereal Crops and Diseases.

TABLE 3.—*Mean pulling resistance and mean values for some associated root characters in the inbred lines and hybrids of maize*

Inbred line or hybrid	Mean values for—								
	Pulling resistance	Dry weight of crown roots [1]	Crown roots [1]	Nodes with roots [1]	Plant height [1 2]	Vertical distance on culm with functional roots [1]	Aboveground nodes with functional roots [1]	Diameter of roots [1 3]	Diameter of culm [1 4]
Inbred lines:	*Pounds*	*Grams*	*Number*	*Number*	*Centimeter*	*Centimeter*	*Number*	*Millimeters*	*Centimeters*
56	227	13.1	60.1	10.1	174	7.6	1.2	2.22	2.16
4-8	209	17.4	78.0	9.3	200	7.6	1.2	2.45	2.62
51	158	8.9	53.6	8.1	197	4.7	.7	2.10	2.22
84	188	13.4	66.3	9.2	141	4.8	1.1	2.02	2.12
Minimum significant difference [5]	39.0	1.3	4.4	.3	6.0	.9	.3	.13	.15
Hybrids:									
56 × 4-8	350	32.0	72.1	9.4	264	8.9	1.7	2.92	3.06
51 × 84	290	23.3	67.5	8.6	245	5.3	1.0	2.77	2.74
(56 × 4-8) × (51 × 84)	333	30.0	72.8	9.1	263	7.1	1.3	2.83	2.94
Minimum significant difference [5]	51.0	3.3	4.8	.4	5.0	1.4	.3	.12	.13

[1] Mean values obtained from samples taken from weeks 12 to 15.
[2] Measured to the tip of the tallest leaf when stretched vertically.
[3] The mean root diameter was obtained by measuring the diameter of one main root at each node at a distance of 15 cm. from the culm.
[4] The diameter of the culm was measured at the middle of the internode immediately beneath the highest node bearing functional roots and was determined as the mean of the smallest and largest diameters.
[5] Minimum difference for significance calculated as twice the standard error of a difference.

TABLE 4.—*Correlation coefficient within strains between pulling resistance and the dry weight of roots and between pulling resistance and the total number of main roots*

Inbred line or hybrid	Correlation coefficient between—		Inbred line or hybrid	Correlation coefficient between—	
	Pulling resistance and dry weights of roots	Pulling resistance and number of roots		Pulling resistance and dry weights of roots	Pulling resistance and number of roots
56	[1] 0.50	0.15	56 × 4-8	0.38	0.18
4-8	[1] .53	−.45	51 × 84	.31	.21
51	[2] .75	−.12	(56 × 4-8) × (51 × 84)	[2] .68	.43
84	[2] .72	.53			

[1] Significant.
[2] Highly significant.

Dry weight of roots was closely associated with pulling resistance (table 3). The only other root character that appeared to be related to pulling resistance among both inbred lines and hybrids was root diameter. Among the inbred lines as a group and the hybrids as a group, the vertical distance on the culm with "functional" roots seemed to bear a relation to pulling resistance. A similar situation existed in regard to the number of nodes with roots. Pulling resistance seemed to be more closely related to the number of above-ground nodes with functional roots among the hybrids than among the inbred lines. Plant height and culm diameter seemed to bear little rela-

tion to pulling resistance among the lines, but among the hybrids the tallest plants with the thickest culms had the greatest pulling resistance.

There was hardly sufficient lodging in the plots during the 1937 season to establish any marked differences among the strains. In lines 56, 4–8, 51, and 84, respectively, 5.5, 2.6, 37.1, and 2.2 percent of the plants lodged at an angle of 45° or greater in November. In hybrids 56×4–8 and 51×84 and the double-cross hybrid, respectively, 0.3, 2.1, and 1.9 percent of the plants lodged. Line 51 failed to remain erect even in a season unfavorable to lodging. This might have been predicted on the basis of its extremely poor root development.

SUMMARY

A comparative study was made of the seasonal development of the corn root system by the use of a double-cross hybrid, two single-cross hybrids, and the four inbred lines employed in making up the hybrids.

The seminal root systems of the hybrids were larger than those of the inbred lines, but in both groups of strains they died early in the growing season, probably because of injuries sustained from various insect larvae and root diseases. There was no consistent correlation, within either group of strains, between the development of the seminal roots and the development of the crown roots or the tops.

Marked differences were noted among the strains in regard to number, dry weight, and total length of the main roots of the crown root systems. The graph of total dry weight of the roots determined at weekly intervals followed a typical S-shaped growth curve. The maximum dry weight of the crown roots was reached at approximately the silking stage in five of the strains and possibly the week following silking for the remaining two strains. It was believed that the inbred lines and hybrids might be expected to show relatively different degrees of resistance to lodging at successive stages of growth on the basis of the growth curves of their roots.

Striking differences were noted among the inbred lines in the ordinary development of lateral roots and in the amount of stimulated lateral root growth following injury of a main root by soil insects.

The top-to-root ratio was nearly 2:1 for some strains at 2 weeks after planting but varied from 12:1 to 23:1 among the strains at 15 weeks after planting. There was no close correlation among the inbred lines between the dry weights of the tops and of the roots.

The single-cross hybrids exceeded the inbred lines in dry weight of roots, dry weight of tops, diameter of main roots, length of roots, resistance to a vertical pull, diameter of culm, and plant height; they tended to approximate the inbred line with the greater number of main roots, but no consistent relation was evident with respect to the number of nodes with roots; they were intermediate between their constituent lines in the top to root ratio during most of the growing season. The double-cross hybrid and one of the single crosses (56×4–8) were nearly identical with respect to most of the root characters studied.

In the plants studied, about one additional whorl of crown roots was developed during each week of the first 8 or 9 weeks of the growing season.

The root systems of both the inbred lines and the hybrids were exceedingly shallow as compared with those reported from the prairie regions of the United States. Data are given for the distribution of the main roots at three different periods during the growing season. Within all strains the number of pounds required to pull a corn plant from the ground was most closely correlated with the dry weight of the crown roots.

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NUTRIENT VALUE OF THE PHOSPHORUS IN DEFLUORINATED PHOSPHATE, CALCIUM METAPHOSPHATE, AND OTHER PHOSPHATIC MATERIALS AS DETERMINED BY GROWTH OF PLANTS IN POT EXPERIMENTS[1]

By K. D. JACOB and WILLIAM H. ROSS, *senior chemists, Fertilizer Research Division, Bureau of Agricultural Chemistry and Engineering, United States Department of Agriculture*[2,3]

INTRODUCTION

In recent years much work has been done on the development of methods for the production of new phosphatic materials suitable for use as fertilizer. Some of these materials, particularly defluorinated phosphate, calcium metaphosphate, and potassium metaphosphate, offer considerable promise as sources of phosphorus for plant growth, either because of their high content of plant food and the consequent economy in transportation and handling costs or because of the possibility of effecting a considerable reduction in processing costs. In either case the primary object of the work is to supply the farmer with cheaper phosphate and at the same time to maintain at a high level the nutrient value of the phosphorus contained therein.

Defluorinated phosphate (prepared by heating phosphate rock at high temperatures in the presence of water vapor and silica) has been produced experimentally in two forms—calcined phosphate and fused phosphate rock—which differ in certain physical characteristics, but which appear to be identical in chemical structure (*28*).[4] Calcined phosphate, obtained in the form of a sintered or semifused, more or less porous clinker, is prepared by defluorinating phosphate rock at temperatures below the melting point of the charge, usually at 1,400° C. (*35*, *46*, *58*, *59*, *60*). Fused phosphate rock, obtained in the form of a hard glassy material, is prepared by defluorinating phosphate rock at temperatures above the melting point of the charge, usually at about 1,550° C. (*12*). Although these products are not produced commerically, they offer interesting possibilities as cheap sources of phosphorus for agricultural purposes, provided certain difficulties that have been encountered in attempts to produce them on a commercial scale can be overcome.

In addition to the adverse effect of incomplete volatilization of the fluorine (*7*, *12*, *32*, *35*, *46*, *58*, *59*), the citrate and citric acid solubilities of the phosphorus of defluorinated phosphate depend, within certain limits, on the particle size of the material (*12*, *34*) and usually on the rate at which the product is cooled from the reaction temperature to atmospheric temperature (*47*). α-Tricalcium phosphate, silicocarnotite ($5\ CaO \cdot P_2O_5 \cdot SiO_2$), and a phase of unknown composition

[1] Received for publication June 15, 1940.

[2] The pot experiments were made by R. P. Bartholomew, Arkansas Agricultural Experiment Station; R. L. Cook, Michigan Agricultural Experiment Station; D. W. Edwards, Hawaii Agricultural Experiment Station; W. T. McGeorge, Arizona Agricultural Experiment Station; W. H. Pierre, West Virginia Agricultural Experiment Station; and F. R. Reid, Bureau of Plant Industry, U. S. Department of Agriculture.

[3] The Fertilizer Research Division was transferred to the Bureau of Plant Industry December 31, 1939.

[4] Italic numbers in parentheses refer to Literature Cited, p. 556.

are the principal constituents of quickly cooled defluorinated phosphates, whereas apatite usually appears as an important constituent in slowly cooled samples (*28*). The material, whether cooled quickly or slowly, contains little or no water-soluble phosphorus.

The researches of the Tennesse Valley Authority (*10, 11*) on calcium metaphosphate and those of the Bureau of Chemistry and Soils on potassium metaphosphate (*40, 41, 45*) have focused attention on the possibilities of these compounds as sources of phosphorus for plant growth, particularly because of their high content of nutrient elements and the consequent economy in handling and transportation costs. Calcium metaphosphate, as prepared by the Tennessee Valley Authority, is obtained by reacting phosphorus pentoxide with phosphate rock at a temperature of 1,200° C. and quickly cooling the product. Potassium metaphosphate can be obtained (1) by heating monopotassium orthophosphate at 700° C., (2) by reacting phosphoric acid with potassium chloride at temperatures up to 850° C., (3) by reacting phosphorus pentoxide and water vapor with potassium chloride, and (4) by smelting a mixture of phosphate rock, potassium silicate, and coke (*27, 55, 56, 64, 65*).

As reported in previous papers (*7, 32*), the results of greenhouse experiments indicated that quickly cooled, finely ground (80- or 100-mesh), low-fluorine calcined phosphate is as effective as superphosphate and dicalcium phosphate in promoting plant growth on soils having pH values below 7. The study reported in the present paper was undertaken to obtain information on the nutrient value of fused phosphate rock, calcium metaphosphate, reverted calcined phosphate, and, particularly, of different particle sizes of unreverted calcined phosphate. Experiments were also made with monocalcium phosphate, dicalcium phosphate, superphosphate, high-grade basic slag, Non-Acid Phosphate (prepared by heating phosphate rock with a potassium salt (*1*)), and ground phosphate rock.

The Arizona, Arkansas, Hawaii, Michigan, and West Virginia Agricultural Experiment Stations and the Bureau of Plant Industry, United States Department of Agriculture, cooperated in the study, the results of which are published in part in another paper (*62*). Although experiments were also made by several other State agricultural experiment stations, the results are not included herein, principally because either the soils did not respond to the phosphate applications, tests were run only on some of the phosphatic materials, or phosphorus determinations were not made on the harvested plants.

REVIEW OF LITERATURE

In agreement with the results previously cited (*7, 32*), Serralles (*67*) reported that quickly cooled, finely ground (80-mesh), low-fluorine (0.10 percent) calcined phosphate was as effective as superphosphate in pot experiments with oats on a phosphorus-deficient Morrison sandy loam soil (pH 6.2) from The Barrens near State College, Pa. Furthermore, the low-fluorine calcined phosphate, in which the citrate solubility of the phosphorus amounted to 92.6 percent, gave somewhat better results than material that contained 0.65 percent of fluorine and showed a 66.4-percent solubility of the phosphorus. Gilbert and Pember (*18*) also used the high-fluorine material in pot tests with barley, buckwheat, and millet on two

Bridgehampton very fine sandy loam soils (pH 4.5 and 6.0, respectively) from the farm of the Rhode Island Agricultural Experiment Station, Kingston, R. I. In general, the results agreed well with those obtained by the use of either monocalcium phosphate, dicalcium phosphate, or double superphosphate.[5] Excellent results have been obtained with calcined phosphate as a source of phosphorus for permanent pasture sod at the New Jersey Agricultural Experiment Station.[6] On the other hand, the results of plot tests by the Idaho station[7] indicate that calcined phosphate, though better than fused phosphate rock, is not as effective as double superphosphate in promoting the growth of alfalfa on alkaline soils. According to Taylor and Pierre,[8] calcined phosphate has a basic action on the soil, whereas ground phosphate rock and natural colloidal phosphate have very little effect in this respect.

In field experiments by the Montana Agricultural Experiment Station (*23*) with cereal crops and alfalfa on phosphorus-deficient alkaline soils, fused phosphate rock produced very small increases in yields as compared to those obtained by the use of water-soluble phosphates (monocalcium phosphate and double superphosphate). Dicalcium phosphate also gave poor results. Likewise, fused phosphate rock was a poor source of phosphorus for the growth of alfalfa and sugar beets in plot experiments by the Idaho station.[7] In a 2-year plot experiment on a Charlton loam soil (pH 5.2) at the Storrs (Connecticut) Agricultural Experiment Station (*6*), the average yield of U. S. Grade No. 1 white potatoes obtained by using fused phosphate rock as the source of phosphorus was 95 percent of that obtained by using double superphosphate. In field trials with corn, wheat, millet, cowpeas, soybeans, and potatoes on several phosphorus-deficient soils, Mooers of the Tennessee Agricultural Experiment Station (*51*) found that fused phosphate rock usually did not give as good results as either monocalcium phosphate, dicalcium phosphate, or double superphosphate. With monocalcium phosphate as 100, the average relative ratings of fused phosphate rock applied to these soils were 97 and 81 as determined by the Neubauer seedling-plant test and by the Cunninghamella test, respectively. The fused phosphate rock used in Mooers' work retained about 25 percent of the fluorine content of the original phosphate rock and the phosphorus therein was probably not more than 50 percent soluble in neutral ammonium citrate solution.

Several high-temperature forms of calcium metaphosphate, differing greatly in their chemical and physical properties, are known. According to Bartholomew and Jacob (*4*), calcium metaphosphate prepared by heating acid-free monocalcium phosphate to constant weight at 600° to 650° C. is insoluble in neutral ammonium citrate solution and practically insoluble in aqua regia, but is soluble in hot concentrated sulfuric acid. In greenhouse experiments, this compound, as well as calcium pyrophosphate prepared by heating pure dicalcium phosphate to constant weight at 800° C., had little or no value as a source of phosphorus for the growth of Sudan grass on Clarksville silt loam

[5] This material, which is made by treating phosphate rock with phosphoric acid, is also known as treble superphosphate, triple superphosphate, or concentrated superphosphate.

[6] SPRAGUE, H. B. Private communication.

[7] LARSON, H. W. E. Private communication.

[8] TAYLOR, J. R., JR., and PIERRE, W. H. THE VALUE OF DIFFERENT BASIC MATERIALS AND OF DOLOMITIC LIMESTONE OF DIFFERENT DEGREES OF FINENESS IN THE PRODUCTION OF NON-ACID-FORMING FERTILIZERS. Amer. Soc. Agron., Com. on Fert., Proc. 1935: 15-23, illus. 1935. [Mimeographed.]

(pH 5.7) at the Arkansas Agricultural Experiment Station (*4*) and for the growth of barley, red clover, and Japanese millet on two Bridgehampton very fine sandy loam soils (pH 4.35 and 6.03) at the Rhode Island station (*18*). At both stations, precipitated calcium pyrophosphate gave much better results than the material prepared by heating dicalcium phosphate. Jolibois and coworkers (*37*) report that calcium metaphosphate which had been crystallized at 500° C. was of no value as a source of phosphorus for the growth of spring barley in pot experiments on alkaline soil (pH 8.1) and of spring oats on acid soil (pH 4.9). Calcium metaphosphate which had been fused and quenched was 57 percent as effective as monocalcium phosphate in increasing the yield on the alkaline soil but was of no value on the acid soil. In pot experiments with several species of plants, Kida (*38*, *39*) found that the fertilizing values of calcium, magnesium, iron, and aluminum metaphosphates and pyrophosphates, prepared by heating the orthophosphates, were lower than those of the respective orthophosphates.

The calcium metaphosphate produced by the Tennessee Valley Authority, by reacting phosphorus pentoxide with phosphate rock at 1,200° C. and quickly cooling the product, is almost completely soluble in neutral ammonium citrate solution according to the official method of analysis (*3*, *pp. 21–22*). Some of the properties of this product were studied by MacIntire, Hardin, and Oldham (*44*), who report that under parallel conditions suspensions of soil, subsoil, ferric oxide, and aluminum oxide in aqueous and ammonium citrate solutions of calcium metaphosphate and orthophosphate, respectively, absorbed decidedly larger quantities of metaphosphate radical (PO_3) than of orthophosphate radical (PO_4). According to Mooers (*51*), field trials with corn, wheat, millet, cowpeas, soybeans, and potatoes on a number of phosphorus-deficient soils in Tennessee showed no significant differences in effects on crop yields between monocalcium phosphate, double superphosphate, dicalcium phosphate, and calcium metaphosphate (prepared by the Tennessee Valley Authority) on the basis of pound for pound of total phosphorus applied. On the other hand, in a comparison of the Neubauer seedling-plant and the Cunninghamella tests as means of obtaining an index of the availabilty of the different phosphates for each of the five types of soil (Colbert, Decatur, Fullerton, Hartsells, and Montevallo), both tests gave ratings to calcium metaphosphate which were usually much lower than those obtained by the field trials. In a 2-year plot experiment on a Charlton loam soil (pH 5.2) at the Storrs (Conn.) Agricultural Experiment Station (*6*), the average yield of U. S. Grade No. 1 white potatoes obtained by using calcium metaphosphate (prepared by the Tennessee Valley Authority) as the source of phosphorus was 95.4 percent of that obtained by using double superphosphate and was practically the same as the yield obtained by using fused phosphate rock. In field trials by the Montana station (*23*), calcium metaphosphate, like fused phosphate rock, was an inefficient source of phosphorus for the growth of cereal crops and alfalfa on phosphorus-deficient alkaline soils. Likewise, calcium metaphosphate, though better than fused phosphate rock, was not, in general, as effective as double superphosphate in increasing the yields of alfalfa, sugar beets, and white potatoes in plot experiments by the Idaho station.[10]

[10] See footnote 7, p. 541.

The nutrient value of the phosphorus in alkali-metal metaphosphates and pyrophosphates has been investigated by several workers. Thus, Weissflog and Mengdehl (*74*) report that monopotassium orthophosphate, potassium metaphosphate and pyrophosphate, and calcium metaphosphate were about equally effective for the growth of corn in sterile culture solutions. Pure salts, the methods of preparation and properties of which are not stated, were used in the experiments. Although corn absorbed the metaphosphates and pyrophosphates, they were subsequently converted quickly into the orthophosphates, and their presence in the plant tissue could be detected only in the roots. In the culture solution itself, the conversion of the metaphosphates and pyrophosphates into the orthophosphates was accelerated by the growth of plants therein. Glixelli and Boratyński (*19*) found no differences in the yields of barley and wheat grown in water cultures containing orthophosphate, pyrophosphate, or metaphosphate, but the absorption of phosphorus was lower from metaphosphate than from either pyrophosphate or orthophosphate. Furthermore, salts of the highly polymerized metaphosphoric acid, prepared by treating the amorphous, difficultly volatile phosphorus pentoxide with water, were absorbed to a smaller degree than were salts of the less polymerized acid, obtained from the crystallized, easily volatile pentoxide.

Burgevin (*31*) conducted water-culture experiments with potassium metaphosphate and orthophosphate, in which vitiation of the results by transformation of metaphosphate into orthophosphate in the cultures was prevented by changing the solutions at 2-day intervals. Under these conditions the compounds were equally effective sources of phosphorus for the growth of corn. Also, he reports (*30*) that commercial potassium metaphosphate gave as good results as monopotassium orthophosphate in pot experiments with spring oats on a nearly neutral soil. When algae were grown in a nutrient solution containing monopotassium orthophosphate, Sommer and Booth (*68*) found that metaphosphate persisted in the living cells after orthophosphate and pyrophosphate could no longer be detected. The transformation of orthophosphate to metaphosphate and the persistence of the metaphosphate indicates that this form is important in the metabolic processes of algae.

In pot experiments on loamy sand and moorland soils (pH 4.4 to 6.5 in aqueous suspension), Krügel, Dreyspring, and Heinrich (*43*) found that Merck's sodium metaphosphate, which was readily soluble in water, contained 68.89 percent P_2O_5, and was probably the hexametaphosphate ($(NaPO_3)_6$), was practically as effective as an equivalent quantity of superphosphate in increasing the growth of winter wheat, yellow oats, winter oats, and winter barley. Bartholomew and Jacob (*4*) conducted pot experiments with potassium metaphosphate and pyrophosphate prepared by heating the pure monopotassium and dipotassium orthophosphates to constant weight at 810° to 820° and at 1,000° C., respectively. Both compounds were somewhat less effective than superphosphate in increasing the weight of Sudan grass grown on Clarksville silt loam (pH 5.7), but they were more effective than superphosphate in increasing the absorption of phosphorus by the plants. In pot experiments at the Rhode Island Agricultural Experiment Station (*18*), the sample of potassium metaphosphate was more effective than monocalcium phosphate in increasing the growth of red clover and Japanese millet on two Bridge-

hampton very fine sandy loam soils having pH values of 6.0 and 4.5, respectively. According to Kida (*38*), sodium metaphosphate and pyrophosphate, prepared by heating the corresponding orthophosphate, were as efficient as the orthophosphates as sources of phosphorus for barley, oats, and wheat grown in pots in Knop's culture medium.

Various processes have been proposed for the manufacture of available phosphates by heating phosphate rock with alkali-metal salts, usually the sulfates or carbonates of sodium and potassium, with or without the addition of silica, or silicates, and other reagents. These processes have been discussed by Fishburne (*15*), Guernsey and Yee (*24*), Messerschmitt (*48, 49*), and Waggaman and Easterwood (*73, pp. 120–132*). As yet, attempts to operate such processes on a commercial scale have not met with sustained success in this country, although the Non-Acid Fertilizer & Chemical Co. and its successor, the Kreiss Potassium Phosphate Co. (*1*), operated plants at Lakeland and later at Tampa, Fla., for several years prior to 1930. In Germany, however, a product known as Rhenania Phosphate (*16, 48, 49*) has been manufactured for more than 20 years by heating phosphate rock with alkali-metal salts under certain conditions. Similar products are manufactured in other European countries. For example, a material, formerly known as Vesta Phosphate (*21*), is produced in Belgium and sold under the name of Supraphosphate or Disintegrated Phosphate (*20, 42*); the same material is known in France as Basiphosphate (*8, 42*). Two products manufactured in Poland are known as Tomasyna and Supertomasyna (*42, 70*), respectively.

In this country Allison, Braham, and McMurtrey (*2*), Conner (*9*), Haskins (*25, 26*), Mooers (*50*), Ross, Jacob, and Beeson (*63*), and Thornton (*72*); in Australia, Teakle, Baron-Hay, and Thomas (*69*), and Thomas (*71*); in South Africa, Dodds (*13*); and in Europe, Erdély (*14*), Gerlach and Nolte (*17*), Graftiau (*20*), Graftiau and Courtoy (*21*), Graftiau, Giele, and Hardy (*22*), Krügel and Drevspring (*42*), Niklas, Schropp, and Scharrer (*52*), Niklas, Strobel, and Scharrer (*53, 54*), Ràth (*57*), Terlikowski and Byczkowski (*70*), Wilhelmj (*75*), and Wilhelmj, Karst, and Gericke (*76*) have shown that citrate-soluble phosphates, prepared by heating phosphate rock with alkali salts, are usually excellent sources of phosphorus for plant growth.

MATERIALS AND EXPERIMENTAL METHODS

The particle size, and the phosphoric oxide (P_2O_5) and fluorine contents [11] of the phosphatic materials used in pot experiments are given in table 1. The phosphoric oxide insoluble in neutral ammonium citrate and 2-percent citric acid solutions, was determined by the official methods (*3, pp. 21-23, 36*). The citrate digestions, but not the citric acid digestions, were made in the presence of filter-paper pulp (*34*).

No. 1 is a commercial superphosphate prepared from Tennessee brown-rock phosphate. Nos. 2 and 3 (reagent quality salts) are monocalcium phosphate monohydrate and partially hydrated dicalcium phosphate, respectively.

Nos. 4 to 10, inclusive, represent different ranges of particle sizes of the same lot of calcined phosphate which was prepared on a semi-works scale by Darling & Co., East St. Louis, Ill., by heating Tennessee

[11] The chemical analyses were made by L. F. Rader, Jr., D. S. Reynolds, and T. H. Tremearne, Fertilizer Research Division, Bureau of Agricultural Chemistry and Engineering.

brown-rock phosphate in an oil-fired rotary kiln at 1,400° C. in the presence of water vapor. Nos. 4, 5, 6, and 7 were prepared by grinding separate quantities of the original calcined phosphate to the indicated degrees of fineness. In these samples (Nos. 4, 5, and 6), the distribution of particle size in the range 20 to 200 mesh is given in table 2.

TABLE 1.—*Phosphatic materials used in pot experiments*

No.	Materia.	Particle size		P_2O_5			Fluorine
				Total	Citrate-insoluble	Citric acid-insoluble	
		Mesh	*Millimeters*	*Percent*	*Percent*	*Percent*	*Percent*
1	Superphosphate	<40	<0.381	[1] 19.67	0.12	4.07	1.25
2	Monocalcium phosphate	<40	<.381	[2] 56.76	.00	.00	.00
3	Dicalcium phosphate	<40	<.381	48.53	2.77	.00	.00
4	Calcined phosphate	<20	<.833	37.40	7.80	4.74	.09
5	do	<40	<.381	37.36	4.72	3.06	.09
6	do	<80	<.175	37.18	3.73	2.77	.09
7	do	<200	<.074	37.20	3.68	2.78	.09
8	do	20–40	0.833–.381	37.30	9.53	5.29	.05
9	do	60–80	.221–.175	37.20	5.63	4.58	.15
10	do	100–150	.147–.104	37.05	4.46	3.44	.13
11	Calcined phosphate, reverted	<80	<.175	37.05	20.50	13.87	.09
12	Basic slag	<100	<.147	18.46	3.61	3.27	<.01
13	Calcium metaphosphate	<80	<.175	63.87	.24	43.83	.12
14	Fused phosphate rock	<80	<.175	28.97	4.60	2.49	.12
15	Non-Acid Phosphate [3]	<100	<.147	26.56	11.40	9.68	2.13
16	Tennessee brown-rock phosphate	<100	<.147	33.75	31.37	27.87	3.64

[1] Contained 12.74 percent of water-soluble P_2O_5.
[2] Contained 54.44 percent of water-soluble P_2O_5.
[3] Contained 2.71 percent of water-soluble K_2O.

TABLE 2.—*Distribution of particle size in calcined phosphates*

No.	Particle size	Distribution of particle size, mesh basis						
		20 to 40	40 to 60	60 to 80	80 to 100	100 to 150	150 to 200	200
	Mesh	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
4	<20	50.2	24.8	7.7	4.3	4.5	3.3	5.2
5	<40	----------	25.7	17.3	10.5	11.3	9.7	25.5
6	<80	----------	----------	----------	9.7	22.5	20.0	47.8

Nos. 8, 9, and 10 were obtained by sieving a quantity of the original calcined phosphate which had been ground to pass a 20-mesh sieve. In portions of these separates which were reground to pass a 200-mesh sieve in order to eliminate the effects of differences in particle size, the variations in the percentages of both citrate- and citric acid-insoluble phosphorus were comparatively small and, in keeping with the results of previous studies (*35*, *46*, *58*, *59*, *60*), were related to the percentages of fluorine in the respective samples (table 3).

As shown by Marshall and coworkers (*47*), defluorinated phosphates, including both calcined phosphates and fused phosphate rocks, which have been cooled rapidly from about 1,400° C. to room temperature are usually much more soluble in neutral ammonium citrate solution than are those which have been cooled slowly through this temperature range. Reversion of the phosphorus to the citrate-insoluble condition is usually much more pronounced in samples cooled in an atmosphere of water vapor than in those cooled in a dry atmosphere. The reverted

calcined phosphate (No. 11) was prepared by heating a portion of No. 6 for 1 hour at 1,000° C. in an atmosphere of water vapor. This treatment decreased the citrate solubility of the phosphorus from 90 to 44.7 percent, but had only a very slight effect on the content of total phosphorus; likewise, the citric acid solubility of the phosphorus decreased from 92.5 to 62.6 percent.

TABLE 3.—*Effect of particle size on solubility of calcined phosphate in neutral ammonium citrate and 2 percent citrate acid solutions*

No.	Particle size [1]	Total P_2O_5	Fluorine	Citrate-insoluble P_2O_5 in sample—		Citric acid-insoluble P_2O_5 in sample—	
				As used	Reground to <200 mesh	As used	Reground to <200 mesh
	Mesh	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
[2] 7	<200	37.20	0.09	3.68	3.68	2.78	2.78
8	20–40	37.30	.05	9.53	2.64	5.29	1.82
9	60–80	37.20	.15	5.63	4.92	4.58	4.36
10	100–150	37.05	.13	4.46	4.29	3.44	3.56

[1] Particle size of material as used in the pot experiments
[2] Representative sample of the original calcined phosphate.

The basic slag (No. 12) is a high-grade imported material. The calcium metaphosphate (No. 13) and the fused phosphate rock (No. 14) were prepared by the Tennessee Valley Authority from Tennessee brown-rock phosphate by the processes described by Curtis and coworkers (*10, 11, 12*). No. 15 (Non-Acid Phosphate) was manufactured in 1925 by the Non-Acid Fertilizer & Chemical Co., Lakeland, Fla., by heating Florida pebble phosphate with a potassium salt (*1*). The Tennessee brown-rock phosphate (No. 16) is a commercial material, sold for direct application to the soil. It was ground so fine that 100, 98, 92, and 86 percent of the material passed 100-, 200-, 300-, and 400-mesh sieves, respectively.

The conditions of the pot experiments are outlined in table 4. For a given series of experiments, the phosphates were applied on the basis of equal quantities of total phosphorus. The plants used in the experiments were German millet (*Setaria italica*), Sudan grass (*Sorghum vulgare* var. *sudanense*), and tomato (*Lycopersicum esculentum*).

TABLE 4.—*Conditions of pot experiments*

Cooperating organization	Soil			Fertilizer applied per pot					Crop [1]				Replications
	Type	pH	Air-dry weight per pot	P_2O_5	Nitrogen		K_2O [2]		Kind	Date of seeding	Plants per pot	Date of harvesting	
					Compound	Weight	Compound	Weight					
			Kilograms	*Grams*		*Grams*		*Grams*			*Number*		*Number*
Arizona Experiment Station.	Calcareous sandy loam [3]	9.5	3.0	[4] 0.50	None		None		Tomato	Feb. 4	51–138	Apr. 15	2
Arkansas Experiment Station, first series.	Clarksville silt loam [5]	5.4	9.0	[6] .27	$(NH_4)_2SO_4$, $NaNO_3$	[7] 0.169	KCl	0.56	Sudan grass	Apr. 9	12	June 8	3
Arkansas Experiment Station, second series.	do.[8]	7.1	9.0	[6] .27	do	[7] .169	KCl	.56	do	do	12	do	3
Bureau of Plant Industry	Norfolk loamy fine sand	5.8	5.0	[9] .60	do	[10] .25	K_2SO_4	[11] .30	German millet	Jan. 21	10	Mar. 24	3
Hawaii Experiment Station.	Dark reddish-brown friable clay.	5.2	5.0	[9] 4.50	NH_4NO_3	1.10	K_2SO_4	1.50	Sudan grass	June 9	40	Sept. 3	2
Michigan Experiment Station.	Miami	5.3	4.0	[4] .152	$(NH_4)_2SO_4$ [12]	.038	KCl [12]	[11] .038	do	Mar. 5	10	May 28	4
West Virginia Experiment Station, first series.	Dekalb silty clay loam [13]	5.3	7.0	[14] .35	$NaNO_3$, urea	[15] .42	KCl	.44	do	May 11	6	July 16	3
West Virginia Experiment Station, second series.	do.[13]	6.1	7.0	[14] .35	do	[15] .42	KCl	.44	do	do	6	do	3

[1] All crops were planted and harvested in 1936.
[2] Excluding K_2O applied in the form of Non-Acid Phosphate, except as indicated.
[3] Semiarid soil, very low in organic matter and containing 3 percent of $CaCO_3$.
[4] Phosphate was thoroughly mixed with the soil.
[5] The soil had been neither fertilized nor limed since 1926.
[6] All fertilizers were thoroughly mixed with the soil on April 3.
[7] 0.097 gm. from $(NH_4)_2SO_4$ and 0.072 gm. from $NaNO_3$.
[8] The soil had been neither fertilized nor limed for at least 18 years.
[9] All fertilizers were thoroughly mixed with the soil just before seeding.
[10] Two-thirds from $(NH_4)_2SO_4$ and one-third from $NaNO_3$.
[11] Including water-soluble K_2O applied in the form of Non-Acid Phosphate.
[12] Applied in solution to the surface of the soil.
[13] The soil had not been limed for 8 years.
[14] Phosphatic and potassic fertilizers were thoroughly mixed with the soil just before seeding.
[15] Equally divided between $NaNO_3$ and urea; 0.35 gm. of nitrogen was thoroughly mixed with the soil just before seeding and 0.07 gm. was applied as a top dressing on July 2.

EFFECT OF PHOSPHATIC MATERIALS ON DRY WEIGHT AND PHOSPHORUS CONTENT OF PLANTS

The average dry weight and phosphorus content of, and recoveries of applied phosphorus in, the plants grown on acid and neutral soils are given in table 5.[12] Data on the tomato plants grown by the Arizona station on a calcareous alkaline soil (pH 9.5) are given in table 6.

TABLE 5.—*Average dry weight and P_2O_5 content of plants and recovery of applied P_2O_5 (acid and neutral soils)*

DRY WEIGHT [1]

Phosphate treatment		German millet, Bureau of Plant Industry [2]	Sudan grass					
			Arkansas Experiment Station [3]		Hawaii Experiment Station [7]	Michigan Experiment Station [8]	West Virginia Experiment Station [4]	
No.	Materia		First series [5]	Second series [6]			First series [9]	Second series [10]
		Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
	No phosphorus	4.2	20.1	11.1	116.4	15.7	12.6	6.6
1	Superphosphate	7.6	24.2	20.0	201.1	23.7	22.7	22.8
2	Monocalcium phosphate	6.8	23.7	19.4	152.1	23.8	22.6	21.0
3	Dicalcium phosphate	8.3	24.9	20.9	188.8	24.7	23.2	23.1
4	Calcined phosphate, <20 mesh	6.3	21.9	18.0	193.6	22.8	21.8	20.4
5	Calcined phosphate, <40 mesh	7.1	24.0	18.0	197.8	24.5	23.5	24.4
6	Calcined phosphate, <80 mesh	7.2	24.0	21.1	194.2	22.2	25.0	23.4
7	Calcined phosphate, <200 mesh	7.8	25.8	20.0	184.9	21.2	24.5	23.7
8	Calcined phosphate, 20 to 40 mesh	6.0	23.6	17.7	173.8	17.9	18.6	18.3
9	Calcined phosphate, 60 to 80 mesh	8.4	21.6	19.2	189.7	23.0	24.6	21.2
10	Calcined phosphate, 100 to 150 mesh	8.7	23.4	20.7	187.3	22.8	23.3	24.5
11	Calcined phosphate, reverted	7.0	22.4	20.7	182.2	22.0	25.2	20.8
12	Basic slag	7.0	23.4	21.7	189.8	10.6	24.0	22.4
13	Calcium metaphosphate	8.1	22.6	21.8	173.2	22.7	25.1	24.5
14	Fused phosphate rock	8.6	23.3	21.3	187.6	21.4	25.7	24.2
15	Non-Acid Phosphate	8.3	23.6	20.8	173.1	21.9	23.7	21.9
16	Tennessee brown-rock phosphate	3.5	20.9	16.3	148.6	19.8	17.8	10.2

P_2O_5 CONTENT [1]

		Milligrams	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*
	No phosphorus	22.1	52.3	34.4	105.9	34.9	34.5	20.9
1	Superphosphate	50.5	59.8	51.2	396.2	58.5	60.6	70.9
2	Monocalcium phosphate	49.8	57.8	49.7	237.3	58.1	65.8	70.1
3	Dicalcium phosphate	64.6	61.5	51.6	390.8	59.5	74.0	66.5
4	Calcined phosphate, <20 mesh	34.6	53.4	50.8	449.2	57.0	65.4	65.5
5	Calcined phosphate, <40 mesh	43.9	61.4	49.5	395.6	52.9	84.4	64.7
6	Calcined phosphate, <80 mesh	47.8	69.1	54.9	462.2	50.8	77.3	80.5
7	Calcined phosphate, <200 mesh	53.6	68.6	57.4	425.3	53.6	68.1	71.1
8	Calcined phosphate, 20 to 40 mesh	32.9	62.1	52.7	460.3	43.7	53.6	61.1
9	Calcined phosphate, 60 to 80 mesh	48.0	58.7	55.9	510.3	53.1	71.3	78.0
10	Calcined phosphate, 100 to 150 mesh	53.8	66.7	55.3	509.5	52.0	82.7	82.8
11	Calcined phosphate, reverted	33.7	63.8	55.7	353.5	49.5	74.3	62.4
12	Basic slag	41.7	69.5	55.8	432.7	46.6	76.8	63.8
13	Calcium metaphosphate	59.3	63.7	52.5	389.7	50.4	80.8	74.2
14	Fused phosphate rock	55.1	63.6	51.3	474.6	47.5	82.5	76.0
15	Non-Acid Phosphate	41.8	64.2	54.9	249.3	46.0	62.6	56.1
16	Tennessee brown-rock phosphate	16.0	55.0	46.8	148.6	42.2	51.3	33.7

[1] Per pot; aerial portions of plants only.
[2] Total P_2O_5 applied at rate of 0.60 gm. per pot (240 pounds per acre); pH of soil 5.8.
[3] Total P_2O_5 applied at rate of 0.27 gm. per pot (60 pounds per acre).
[4] Total P_2O_5 applied at rate of 0.35 gm. per pot (100 pounds per acre).
[5] pH of soil 5.4.
[6] pH of soil 7.1.
[7] Total P_2O_5 applied at rate of 4.5 gm. per pot (1,300 pounds per acre); pH of soil 5.2.
[8] Total P_2O_5 applied at rate of 0.152 gm. per pot (76 pounds per acre); pH of soil 5.3.
[9] pH of soil 5.3.
[10] pH of soil 6.1.

[12] Most of the phosphorus determinations were made by T. H. Tremearne, Fertilizer Research Division, Bureau of Agricultural Chemistry and Engineering.

TABLE 5.—*Average dry weight and P_2O_5 content of plants and recovery of applied P_2O_5 (acid and neutral soils)*—Continued

RECOVERY OF APPLIED P_2O_5[1]

No.	Phosphate treatment: Material	German millet, Bureau of Plant Industry	Sudan grass: Arkansas Experiment Station, First series	Arkansas Experiment Station, Second series	Hawaii Experiment Station	Michigan Experiment Station	West Virginia Experiment Station, First series	West Virginia Experiment Station, Second series
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
1	Superphosphate	4.7	2.7	6.2	6.5	15.5	7.5	14.3
2	Monocalcium phosphate	4.6	2.0	5.7	2.9	15.3	8.9	14.1
3	Dicalcium phosphate	7.1	3.4	6.4	6.3	16.2	11.3	13.0
4	Calcined phosphate, <20 mesh	2.1	.4	6.1	7.6	14.5	8.8	12.7
5	Calcined phosphate, <40 mesh	3.6	3.4	5.6	6.4	11.8	14.3	12.5
6	Calcined phosphate, <80 mesh	4.3	6.2	7.6	7.9	10.5	12.3	17.0
7	Calcined phosphate, <200 mesh	5.3	6.0	8.5	7.1	12.3	9.6	14.3
8	Calcined phosphate, 20 to 40 mesh	1.8	3.6	6.8	8.1	5.8	5.5	11.5
9	Calcined phosphate, 60 to 80 mesh	4.3	2.4	8.0	9.0	12.0	10.5	16.3
10	Calcined phosphate, 100 to 150 mesh	5.3	5.3	7.7	9.0	11.3	13.8	17.7
11	Calcined phosphate, reverted	1.9	4.3	7.9	5.5	9.6	11.4	11.9
12	Basic slag	3.3	6.4	7.9	7.3	7.7	12.1	12.3
13	Calcium metaphosphate	6.2	4.2	6.7	6.3	10.2	13.2	15.2
14	Fused phosphate rock	5.5	4.2	6.3	8.2	8.3	13.7	15.7
15	Non-Acid Phosphate	3.3	4.4	7.6	3.0	7.3	8.0	10.1
16	Tennessee brown-rock phosphate	−1.0	1.0	4.6	.9	4.8	4.8	3.7

[1] Per pot; aerial portions of plant only.

TABLE 6.—*Effect of phosphatic materials on tomato plants grown on soil having a pH value of 9.5* [1]

No.	Material	Plants per pot	Color of plants	Condition of plants	Dry weight per 100 plants	P_2O_5 content per 100 plants	Efficiency of phosphatic material as indicated by increase in—: Dry weight of 100 plants[2]	Efficiency of phosphatic material as indicated by increase in—: P_2O_5 content of 100 plants[2]
		Number			*Grams*	*Milligrams*		
	No phosphorus	122	Purple	Poor	4.1	17.8		
1	Superphosphate	80	Green	Good	9.3	75.4	100	100
2	Monocalcium phosphate	51	do	do	11.0	93.5	133	131
3	Dicalcium phosphate	74	Purple	Poor	7.1	41.9	58	42
4	Calcined phosphate, <20 mesh	87	do	do	8.4	42.1	83	42
5	Calcined phosphate, <40 mesh	88	do	do	7.6	51.6	67	59
6	Calcined phosphate, <80 mesh	87	do	do	7.8	35.2	71	30
7	Calcined phosphate, <200 mesh	81	do	do	9.8	48.9	110	54
8	Calcined phosphate, 20 to 40 mesh	138	do	do	8.2	27.8	79	17
9	Calcined phosphate, 60 to 80 mesh	101	do	do	5.9	21.5	35	6
10	Calcined phosphate, 100 to 150 mesh	88	do	do	4.8	24.0	13	11
11	Calcined phosphate, reverted	109	do	do	5.4	23.6	25	10
12	Basic slag	102	do	do	6.5	38.4	46	36
13	Calcium metaphosphate	69	do	do	6.7	74.5	50	98
14	Fused phosphate rock	130	do	do	5.4	30.7	25	22
15	Non-Acid Phosphate	91	do	do	7.7	57.6	69	69
16	Tennessee brown-rock phosphate	91	do	Very poor	4.0	27.2	−2	16

[1] Experiments by Arizona Agricultural Experiment Station on a semiarid, sandy loam soil that was very low in organic matter and contained 3 percent of $CaCO_3$.

[2] Based on the increase from superphosphate as 100.

In the acid and neutral soils (table 5), marked increases in the growth and the phosphorus content of the plants were nearly always obtained with all the chemically processed phosphates. Although it was usually considerably less effective than the other phosphatic mate-

rials in a given series of experiments, increases in the dry weight anp the phosphorus content of the plants were also obtained by the application of ground phosphate rock (No. 16), except in the experiments by the Bureau of Plant Industry.

A fair comparison of the relative effects of the phosphates applied to the alkaline soil (table 6) cannot be obtained, because the number of plants grown per pot varied widely. In agreement with investigations by the Idaho [13] and Montana (*23*) Agricultural Experiment Stations, the data indicate, nevertheless, that the so-called water-insoluble phosphates are not good sources of phosphorus for the growth of plants on alkaline soil. The results are said to be in accord with the usual experience with Arizona soils.[14] It will be noted that the plants which received calcium metaphosphate (No. 13) showed a high absorption of phosphorus, but this was not accompanied by any marked improvement in their condition and color. Because of the lack of uniformity in the experimental procedure, this series of experiments will be excluded from further discussion.

In previous tests comparing calcined phosphates, which varied widely in fluorine content and likewise in ammonium citrate- and citric acid-soluble phosphorus, the effect of the materials on the phosphorus content of the plants in a given series of experiments was, with a few exceptions, in the same order as their effect on the dry weight (*32*). When all the samples used in the present tests (table 5) are considered on the basis of the increase in the dry weight of the plants, the relative order of the phosphatic materials in a given series of experiments in many instances differs rather widely from that based on the phosphorus content of the plants. If, however, the samples involving the different ranges of particle size of the calcined phosphate (Nos. 4, 5, 7, 8, 9, and 10) are excluded, the agreement is very much better, and both bases of comparison usually place the materials in either the same or nearly the same relative order.

Scarseth and Chandler (*66*) studied the residual phosphate situation with a nearly level Norfolk loamy sand in Alabama which had been used for a 26-year period in an experiment involving a 3-year rotation of cotton, corn, and oats with various legumes and with different phosphatic fertilizer treatments. Where superphosphate was used, 32 percent of the applied phosphorus was utilized by the plants, 8 percent remained in the soil, and 60 percent was carried away with the clay fractions lost by erosion. With ground phosphate rock the corresponding figures were 9, 9, and 82, percent, respectively. As indicated by the phosphorus content of the aerial parts of the plants, the recovery of the applied phosphorus in the present experiments usually did not exceed 10 percent, and in no case was it as high as 20 percent (table 5). With one exception (calcined phosphate No. 4, Arkansas station, first series), the recoveries of phosphorus from ground phosphate rock (No. 16) were lower, usually very much lower, than those from the other materials. With the same type of soil and the same weight of applied phosphorus, the recoveries of phosphorus from all the materials, except ground phosphate rock at the West Virginia station, increased with the pH value of the soil (Arkansas and West Virginia stations). Contrary to the results of previous

[13] See footnote 7, p. 541.

[14] McGeorge, W. T. Private communication. Arizona Agricultural Experiment Station.

experiments (*32*), there was no relation between the recovery and the per acre rate of application of the phosphorus.

RELATIVE EFFICIENCY OF PHOSPHATIC MATERIALS

The relative efficiency of the different types of phosphates, as indicated by the increase in the dry weight and phosphorus content of plants grown on acid and neutral soils, is shown in figure 1, and similar data for the different ranges of particle sizes of the calcined phosphate (Nos. 4 to 10, inclusive) are shown in figure 2. The efficiency of the phosphates is based upon 100 as the increase in dry weight or phosphorus content due to the application of superphosphate. The Bureau of Plant Industry used German millet as the test crop; the experiment stations used Sudan grass. In figure 1, the materials differ not only in the chemical nature of the phosphorus-bearing compound or compounds but usually in their content of calcium and other elements, as well as in their basicities and hence in their ability to neutralize soil acids. Therefore, the changes in the plant dry weights and phosphorus content obtained with these materials do not necessarily represent merely the specific effects of the applied phosphorus. In figure 2, on the other hand, the compared materials are practically identical in chemical composition, and the differences in their efficiency can be attributed entirely to particle-size effects.

Although for a given material the efficiencies based on the dry weight of the plants show rather wide variations in some instances, they are usually much more consistent than those based on the phosphorus content. Furthermore, for a given material in a given series of experiments, the efficiency based on the dry weight is usually lower, often very much lower, than that based on the phosphorus content, which is contrary to the results of previous experiments (*32*).

On the basis of the dry-weight increases, the average relative efficiency of the different types of phosphatic materials (fig. 1) falls in the decreasing order: Dicalcium phosphate, 107; fused phosphate rock, 102; superphosphate, 100; <80-mesh calcined phosphate, 99; calcium metaphosphate, 98; Non-Acid Phosphate, 95; basic slag, 90; reverted calcined phosphate, 88; monocalcium phosphate, 84; and Tennessee brown-rock phosphate, 31. On the basis of the increases in phosphorus content of the plants, the order is: <80-mesh calcined phosphate, 130; fused phosphate rock and calcium metaphosphate, 120; basic slag, 119; dicalcium phosphate, 117; superphosphate and reverted calcined phosphate, 100; monocalcium phosphate and Non-Acid Phosphate, 89; and Tennessee brown-rock phosphate, 32. Although the two bases of comparison do not place the efficiencies of the materials (except those of fused phosphate rock and ground phosphate rock) in the same order, both bases give high ratings to dicalcium phosphate, fused phosphate rock, <80-mesh calcined phosphate, and calcium metaphosphate and a comparatively low rating to ground phosphate rock.

In nearly all the tests dicalcium phosphate was equal or superior to superphosphate as a source of phosphorous for the growth of plants on acid and neutral soils. Good results were also obtained with this material in previous experiments (*32*, *61*, *63*). On the other hand, monocalcium phosphate was usually less efficient than superphosphate (fig. 1). In view of the high average efficiency of the dicalcium phos-

phate, <80-mesh calcined phosphate, fused phosphate rock, and calcium metaphosphate (materials which are either very low in or free from sulfur) as compared with that of the sulfur-rich superphosphate,

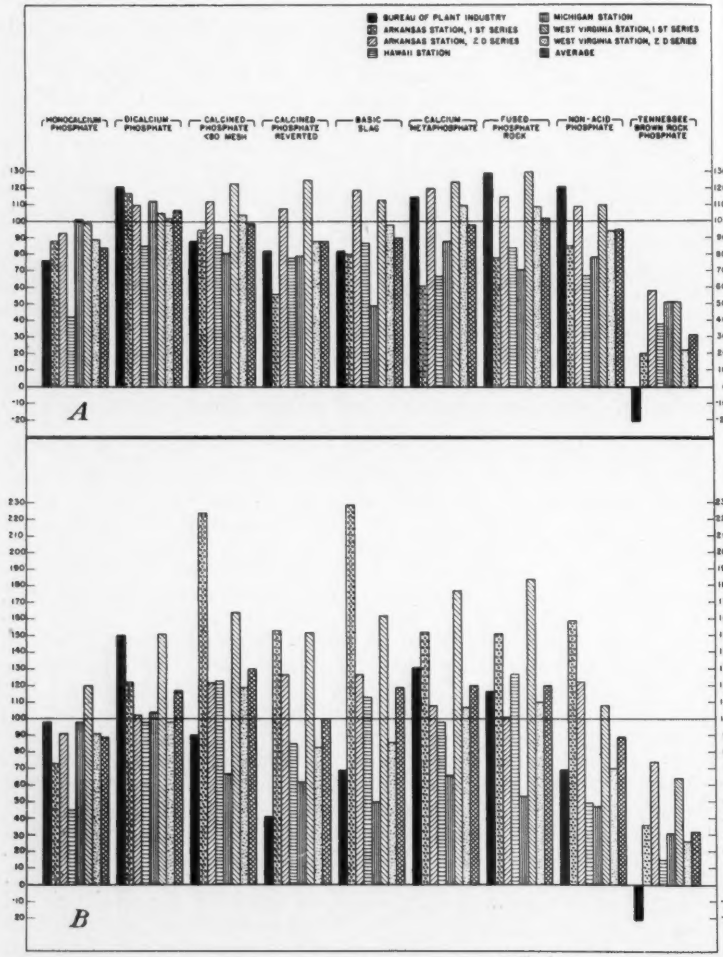

FIGURE 1.—Relative efficiency of different types of phosphatic materials, as indicated by increase in dry weight and phosphorus content of plants grown on acid and neutral soils, based on the increase from superphosphate as 100: *A*, Efficiency of phosphate as indicated by increase in dry weight; *B*, efficiency of phosphate as indicated by increase in phosphorus content of plants.

the relatively low efficiency of the monocalcium phosphate cannot be attributed to the absence of sulfur therefrom.

As shown in figure 1, the average efficiency of the Non-Acid Phosphate in increasing the dry weight of the plants was slightly higher

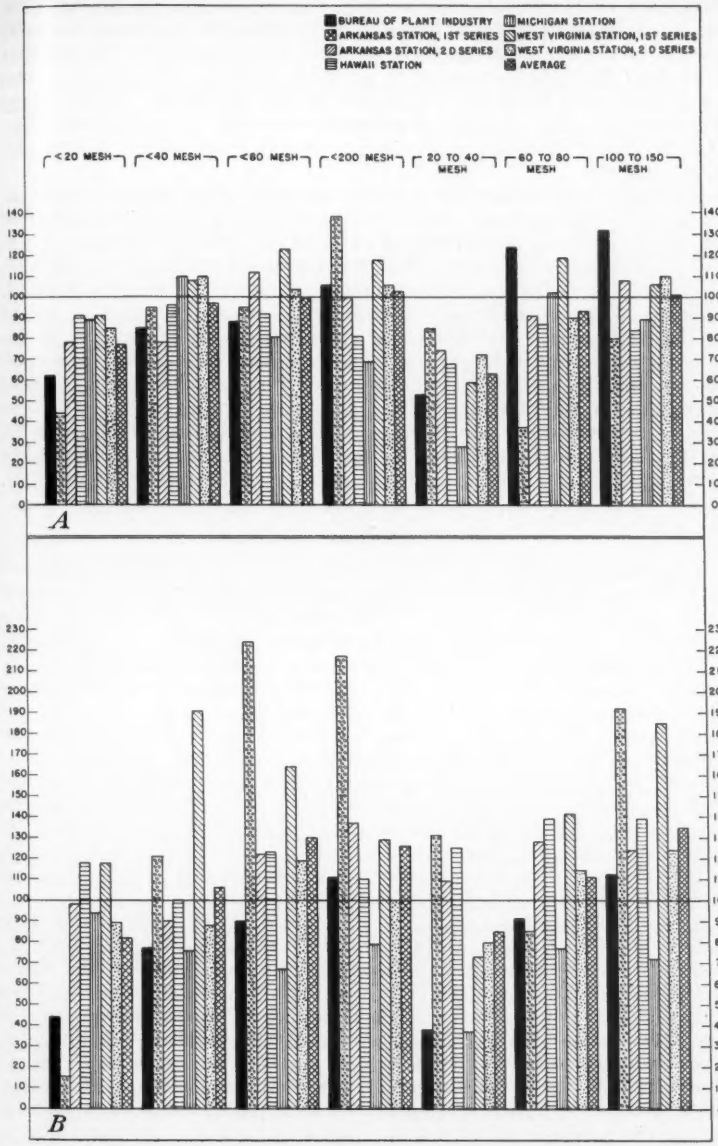

FIGURE 2.—Relative efficiency of different particle sizes of calcined phosphate as indicated by increase in dry weight and phosphorus content of plants grown on acid and neutral soils, based on the increase from superphosphate as 100: *A*, Efficiency of phosphate as indicated by increase in dry weight of plants; *B*, efficiency of phosphate as indicated by increase in phosphorus content of plants.

than that of the imported basic slag. In other experiments with the same materials (*63*),[15] the efficiency was in the reverse order. In tests by the Neubauer seedling-plant method, Thornton (*72*) [15] found that Non-Acid Phosphate, applied to an acid silt loam soil (pH 5.4), was 79 to 85 percent as effective as monocalcium phosphate. The average efficiency of reverted calcined phosphate was significantly lower than that of the <80-mesh unreverted material from which it was prepared (fig. 1).

Although the results for a given material vary rather widely in some cases, the average efficiency (fig. 2) shows clearly the effect of the particle size on the fertilizing value of calcined phosphate. Thus, the average efficiency of the material increased markedly as the fineness of the particles was increased from 100 percent through a 20-mesh sieve to 100 percent through a 40-mesh sieve, and to a smaller extent as the particle size was decreased still further. Likewise, 20- to 40-mesh particles were, in general, considerably less efficient than were 60- to 80-mesh particles, and the latter were somewhat less efficient than 100- to 150-mesh material. It appears, however, that little is gained by increasing the fineness of calcined phosphate beyond 80 mesh. The average efficiency of the 80-mesh product was somewhat lower than that of similar material used in previous experiments (*32*).

COMPARATIVE EFFICIENCY AND SOLUBILITY OF PHOSPHATIC MATERIALS

The average relative efficiency of most of the materials, as indicated by the increases in the dry weights of plants grown on acid and neutral soils, was higher than would be expected on the basis of their solubility in neutral ammonium citrate solution (table 7). In particular, the average responses to applications of reverted calcined phosphate and of Non-Acid Phosphate were very much higher than the respective citrate solubilities of the phosphorus contained therein. On the other hand, the average efficiencies (indicated by increases in dry weights) of the monocalcium phosphate, <20-mesh calcined phosphate, 20- to 40-mesh calcined phosphate, and calcium metaphosphate were somewhat lower than the respective citrate solubilities of the phosphorus. The average efficiency of the different ranges of particle sizes of the calcined phosphate (Nos. 4 to 10, inclusive) was usually in the same order as the solubility of the phosphorus in either neutral ammonium citrate or 2-percent citric acid solution.

Aside from the monocalcium phosphate, which was completely soluble in either solvent, all but two of the materials (superphosphate and calcium metaphosphate) showed higher solubility of the phosphorus in citric acid than in ammonium citrate. Previous studies (*4*, *5*, *29*, *33*) have shown that iron and aluminum orthophosphates are more soluble in neutral ammonium citrate solution than in 2-percent citric acid, whereas the reverse is true of the calcium orthophosphates (*32*, *33*, *36*). As compared to the citrate solubility, the lower citric acid solubility of the phosphorus in superphosphate is no doubt due to the presence of iron or aluminum phosphates, or both. Since the conditions under which the sample is treated for the determination of citrate-soluble phosphorus (*3*, *pp. 21–22*) are more favorable for the hydrolysis of metaphosphate to orthophosphate than those in the determination of citric acid-soluble phosphorus (*3*, *p. 36*), the greater solubility of the calcium metaphosphate in the first solvent

[15] In this paper, Non-Acid Phosphate was called calcined phosphate.

is probably due principally to a higher conversion into orthophosphate during the digestion of the sample and the filtration of the extract.

TABLE 7.—*Comparative efficiency and solubility of phosphatic materials*

No.	Material	Average efficiency of phosphatic material as indicated by increase in—		Solubility of phosphatic material as determined by—	
		Dry weight of plants [1]	Phosphorus content of plants [1]	Neutral ammonium citrate method [2]	2-percent citric acid method [2]
				Percent	*Percent*
1	Superphosphate	100	100	99.4	79.3
2	Monocalcium phosphate	84	89	100.0	100.0
3	Dicalcium phosphate	107	117	94.3	100.0
4	Calcined phosphate, <20 mesh	77	82	79.1	87.3
5	Calcined phosphate, <40 mesh	97	106	87.4	91.8
6	Calcined phosphate, <80 mesh	99	130	90.0	92.5
7	Calcined phosphate, <200 mesh	103	126	90.1	92.5
8	Calcined phosphate, 20 to 40 mesh	63	85	74.5	85.8
9	Calcined phosphate, 60 to 80 mesh	93	111	84.9	87.7
10	Calcined phosphate, 100 to 150 mesh	101	135	88.0	90.7
11	Calcined phosphate, reverted	88	100	44.7	62.6
12	Basic slag	90	119	80.4	82.3
13	Calcium metaphosphate	98	120	99.6	31.4
14	Fused phosphate rock	102	120	84.1	91.4
15	Non-Acid Phosphate	95	89	57.1	63.6
16	Tennessee brown-rock phosphate	31	32	7.1	17.4

[1] Based on the increase from superphosphate as 100, excluding results obtained with alkaline soil by the Arizona Agricultural Experiment Station.
[2] Based on the total phosphorus content of the material.

All the experiments with calcium metaphosphate (fig. 1 and table 7) show that its value as a source of phosphorus for the growth of plants on acid and neutral soils is correlated much more closely with the solubility of the phosphorus in neutral ammonium citrate solution than in 2-percent citric acid. In agreement with the results of previous studies (*32*, *36*), on the other hand, the citric-acid method seems to give a better index of the values of finely ground calcium orthophosphates as sources of phosphorus for the growth of plants on such soils than does the neutral ammonium citrate method. Although the evidence at hand is insufficient to justify a definite conclusion, it appears that neither method is satisfactory for the evaluation of phosphates for application to alkaline soil (table 6) and that water-soluble phosphates are the best sources of phosphorus for plant growth on such soil.

SUMMARY

In order to obtain information on the nutrient value of the phosphorus in defluorinated phosphates (calcined phosphate and fused phosphate rock) and the high-temperature form of calcium metaphosphate, pot experiments were made with Sudan grass and German millet on Clarksville silt loam, Norfolk loamy fine sand, Miami soil, Dekalb silty clay loam, and a dark reddish-brown friable clay, ranging in pH from 5.2 to 7.1, and with tomatoes on a calcareous sandy loam of pH 9.5. Particular attention was given to the nutrient value of calcined phosphate as affected by the particle size of the material. Experiments were made with reverted calcined phosphate in which a considerable portion of the phosphorus had been converted into forms insoluble or only partly soluble in neutral ammonium citrate

and 2-percent citric acid solutions by heating the soluble material at 1,000° C. in the presence of water vapor. Superphosphate, monocalcium phosphate, dicalcium phosphate, high-grade basic slag, ground raw phosphate rock, and Non-Acid Phosphate (prepared by heating a mixture of phosphate rock and a potassium salt at high temperature) were also included in the tests.

In general, finely ground unreverted calcined phosphate (<80 mesh, or finer), fused phosphate rock, and calcium metaphosphate were approximately equal to superphosphate as sources of phosphorus for the growth of plants on acid and neutral soils, but the results of a single series of experiments indicated that these materials, as well as the other types of water-insoluble phosphates, are not so effective as water-soluble phosphates (monocalcium phosphate and superphosphate) on alkaline soils.

The average efficiency of the phosphorus of unreverted calcined phosphate increased markedly as the fineness of the particles was increased from 100 percent through a 20-mesh sieve to 100 percent through a 40-mesh sieve, and to a smaller extent as the particle size was decreased still further. Likewise, 20- to 40-mesh particles were, in general, considerably less efficient than 60- to 80-mesh particles, and the latter were somewhat less efficient than 100- to 150-mesh material. It appears, however, that little is gained by increasing the fineness of calcined phosphate beyond 80 mesh.

The average efficiency of reverted calcined phosphate and Non-Acid Phosphate in increasing the growth of plants on acid and neutral soils was much higher than would be expected on the basis of the citrate and citric acid solubility of the phosphorus contained therein. The average efficiency of calcium metaphosphate was much higher than its solubility in 2-percent citric acid indicated, but was in good agreement with its solubility in neutral ammonium citrate solution. With this material, superphosphate, and the coarsely ground unreverted calcined phosphate (<20-mesh and 20- to 40-mesh materials) as exceptions, the solubility of the phosphorus in 2-percent citric acid appeared, in general, to give a somewhat better index of the values of the phosphatic materials for the growth of plants on acid and neutral soils than did the solubility in neutral ammonium citrate.

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